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SWEET CORN IN JALISCO

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Any careful inquiry into the origin of a cultivated plant presents a twofold problem: the origin of the plant and the origin of its use. These two lines of inquiry yield two different kinds of evidence whose relative importance may vary greatly from crop to crop. It may even vary for different kinds of the same crop, as for example, dent corn and sweet corn, two characteristic forms of *Zea Mays*.[1] For dent corn the genetical situation is complex; the cultural one is simple.[2] For sweet corn, the opposite is true. Therefore, genetical evidence is more decisive in studying the origin of the former, cultural evidence in studying the latter.

As Erwin ('31, '42) has pointed out, the origin of sweet corn presents no particular problem genetically. Though there is more than one allelomorph of the gene for sweet and though in some stocks of maize a genetically sweet kernel will give little outward indication of that fact, the difference between sweet and non-sweet is a single gene difference. Sweet corn, therefore, can arise spontaneously from any ordinary maize; it is possible and even probable that sweet corns may have originated in various places and at various times.

Culturally, however, the story is more complex. While the change is a simple one genetically, it presents the maize grower with a product quite different from that which he had previously. Unlike the change from flinty to floury or from

[1] The word "corn" is used throughout this paper to refer to maize *(Zea Mays)*. While the latter term customarily is used in scientific papers because of its greater precision, its adoption here would result in the unnatural compound "sweet maize", a term which never is heard in the regions where "sweet corn" is grown.

[2] Dents differ from non-dents by a very large number of genes (Hayes, '12). The genetical story is a complicated one, but once it is understood we shall have critical evidence concerning the origin of dent corns from their presumably undented ancestors. A slightly dented variety will differ but little from flour corn in composition or texture; a strongly dented kernel will be almost like a flint. Among the various varieties of corn grown by the Indians of the American Southwest the undented and "semi-dented" varieties often are used for the same purposes, and many of the varieties show a mixture of undented and slightly dented ears. Accordingly, cultural data will have relatively little bearing on the history of the dent corns.

non-dent to dent, this mutation produces a kernel which for most purposes is decidedly inferior to that of non-sweet maize. At the same time, it produces a kernel which can be used in various new ways when once its capabilities are recognized.

Sweet corn is therefore a peculiar product which usually must be, and frequently is, used in special ways. Although the cultural evidence is somewhat diverse, eventually it should cast light on the early history or histories of sweet corn as a cultivated crop. The present paper does not attempt to discuss this general problem; it merely presents as fully as possible the evidence concerning the morphology, the cytology, the distribution, and the uses of sweet corn in Jalisco, Mexico. When similar information is available from other critical areas, it should then be possible to attack the larger problem.

MORPHOLOGY

Fig. 1. Longitudinal section of a kernel of Jaliscan sweet corn. Stippled area indicates embryo. In endosperm, black indicates sugary and white indicates starchy.

A detailed summary of ear, cob, and kernel characters in our collections is presented in table 1 (see Anderson and Cutler, '42), and typical ears are illustrated in pl. 4. It will be seen that the grains, while similar in general appearance to commercial varieties of sweet corn, are characteristically not quite so shrunken. This impression is confirmed when the kernels are examined histologically. The endosperm is not completely sugary but has starch stored at the base as shown in fig. 1. It is therefore unlike the sweet corns of the United States, which ordinarily have no such basal starch zone. Mangelsdorf and Reeves have given a preliminary report ('39, p. 257) on these Mexican sweet corns. They are apparently due to another allelomorph of the gene for sweet and are further affected by a modifying gene in the tenth chromosome. The tests necessary to work out the exact genetic constitution of Jaliscan sweet corn would be difficult to make in the United States since these varieties have a very long growing season.

The color of the dried kernels varies from a bright orange-yellow to deep red. The endosperm is yellow, and the various shades of orange and red result from varying amounts of color in the pericarp. We have neither seen nor heard of a white sweet corn in Jalisco although this color is common among flour corns, dent corns, and popcorns in that area. Sweet corn sometimes is said to be "*negro*", but this probably refers to the dark red ears; a dark red flint from Unión de Tula is called "*maiz negro*" merely because it is dark-colored when cooked.

TABLE I

SUMMARY OF EAR, COB, AND KERNEL CHARACTERS IN JALISCAN SWEET CORN

("s" indicates that a character is strongly developed; "w" that it is present but not extreme. All measurements in centimeters.)

Locality	Ear length	Mid-ear width	Shank diameter	Row number	Row width	Kernel thickness	Husk striation	Base compression	Color
Unión de Tula	14	5.2	1.4	20	.9	.4	w	s	Red
Unión de Tula	16	4.6	1.6	16	.9	.4	w	s	Light orange
C. Guzmán	13	5.1	1.9	16	1.0	.5	s	s	Red
C. Guzmán	16	5.7	1.7	20	.9	.4	w	s	Dark orange
Ameca	20	4.9	2.2	16	1.0	.4	w	s	Dark red
Ameca	19	4.7	1.8	20	.8	.5	s	s	Orange
Ameca	18	4.3	1.8	12	1.2	.5	s	s	Yellow

Ten to fifteen plants were grown from each of the three ears collected at Las Canoas, near El Chante, Autlán. They were planted at the Blandy Experimental Farm of the University of Virginia, at Boyce, Virginia, in early May and did not flower until the middle of September. In long season, as well as in other ways, they were very similar to the characteristic small-kernelled flints or popcorns of Jalisco which bear a general resemblance to most of the "hot country" varieties of maize from the Colorado River to the deserts of Chile. Detailed measurements are presented in table II. In general, the plants were tall, slender, and tough. The internode diagram of a typical plant is illustrated in fig. 2. Tillers were frequent and often numerous (see table II), and the tillers were morphologically so like the main stalk that by the time the plants had begun to tassel it was often difficult to tell which was the primary shoot and which were secondaries.[3] The leaves were slender and tough and were undamaged in windstorms which played havoc with collections from Guatemala and from Michoacán.

TABLE II

SUMMARY OF PLANT AND TASSEL CHARACTERS FOR 3 EAR-TO-ROW TESTS OF JALISCAN SWEET CORN

Plant No.	Tiller Number			Number of tassel branches	Glume length in cm.	% condensed internodes	% sub-sessile spikelets
	Min.	Ave.	Max.				
24a	1	4	5	27	1.2	10	0
24b	0	2	3	31	1.1	0	0
24c	0	2	3	21	1.1	30	0

[3] It must be noted that several traits exhibited in the experimental plantings are not characteristic of sweet corn when it is grown locally in Jalisco. In the first place, the remarkable tillering qualities above described are abnormal. In Jalisco, sweet corn, and other maize varieties as well, ordinarily produces a single stalk; for this reason several kernels are planted together. In the second place, the rare secondary stalks which appear are easily distinguishable from the primary shoot since they remain somewhat stunted. In the third place, in Jalisco, sweet corn does not require an excessively long season but ripens coincidentally with most other types of maize; green ears are available approximately three months after planting. However, dent corn from Michoacán did not tiller when grown in Virginia, nor did it require such a long growing season.

The ears characteristically were shorter, thicker, and more rounded than those of other Jaliscan maize. They bulged in the middle rather than tapering sharply and evenly like most Mexican maize. Since cob shape depends upon a very large number of genes, it is one of the best criteria of relationship. It is therefore significant that Jaliscan sweet corns tend very strongly to have a cob shape which is different not only from other Jaliscan maize but also from most other Mexican

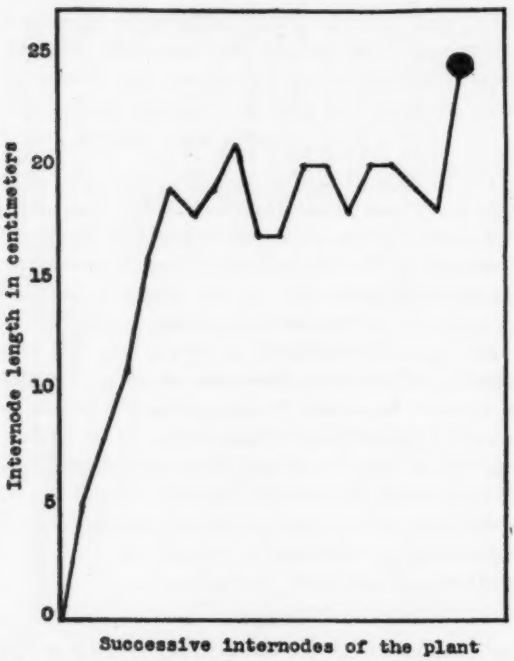

Fig. 2. Internode diagram of a typical plant of Jaliscan sweet corn as grown at Blandy Farm. Circle represents the tassel.

maize. It is, however, a shape which is common in parts of South America and which also occurs in Guatemala. In this connection it is interesting that when the kernel color pattern is revealed by contamination with starchy corn (pericarp colors are difficult to distinguish on a background of sweet endosperm) it is one which is common in Guatemala but very rare in most of Mexico, being deep red at the base and fading towards the top so that the yellow endosperm shows through.

The leaves were practically glabrous, with only a few long scattered hairs at the top of the sheath, and both leaves and stems were a bright, shiny green, with only a trace of anthocyanin pigment. By the time the plants were well developed they were so slender, green, and tough, and there were so many tillers, that they

resembled a bamboo thicket rather than a field of North American sweet corn. The tassels developed so late in the season that their development was probably somewhat abnormal. However, they seemed to be similar to most other Jaliscan maize in having large open tassels with many widely separated branches and large coarse glumes. Anthers and silks were uniformly green.

Conclusions from morphological data.—In general, Jaliscan sweet corn is similar to the other maize of that region and is particularly close to the slender, small-grained popcorns which apparently have been there for a very long time. Its most important differences are the larger, broader, more rounded ear and the peculiar red and yellow color. The cob size and shape are comparatively uniform from collection to collection, and there is less color variation than among other kinds of Jaliscan maize. Its uniformity and its slight but constant cob differences suggested that Jaliscan sweet corn may have originated elsewhere. In any case, it appears either to have been extensively mixed with Jaliscan maize or to have originated from a closely related stock.

CYTOLOGY

Pachytene acetocarmine smears were made from one plant at the Blandy Experimental Farm. The data are summarized in table III. While they will be much more significant when our knowledge of knob number and distribution in various races of corn is more complete, they already confirm the above conclusions derived from pure morphology. In general, the distribution of the knobs and their number and size are like those of other Jaliscan maize, the two small sub-median knobs on the sixth chromosome and the very large terminal knob on the ninth being particularly characteristic.

TABLE III

KNOB NUMBER AND DISTRIBUTION IN JALISCAN SWEET CORN

("s" indicates a small knob, "T" a terminal knob.)

Chromosome Number	1	2	3	4	5	6	7	8	9	10
Average for Jalisco (non-sweet)	0	1	1	1	1	3 (2s)	1	0	T	0
No. 25	0	1	1s	1s	1	3 (2s)	1	0	T	0

DISTRIBUTION AND USES

Sweet corn, or *maiz dulce,* as it is known in Mexico, is general throughout the state of Jalisco, although it is not grown on a large scale. It has a wide altitudinal zonation, from La Huerta, in the Purificación, to El Jazmín, and throughout the Los Altos zone.[4] No information is available from the Pacific seaboard (Puerto

[4] Actual elevations are not readily ascertainable. The 1926 Scanlon map, published by the Secretaría de Agricultura y Fomento, indicates that La Huerta has an approximate elevation of 500 m., whereas the Los Altos district ranges from 1500 to 2000 m.

Vallarta, Tomatlán, Sihuatlán, etc.), but it may be predicted confidently that sweet corn will be found in this coastal stretch. In fact, of the areas of Jalisco which we know, only the upland, almost sub-alpine, district of Tapalpa is said definitely to lack *maiz dulce*. The latter evidently has a considerable tolerance to cold since it is grown in the more sheltered spots about El Jazmín, on the north flank of the Volcán de Colima, where maize and beans alike require six months to mature.

Collections have been made in the following areas: Ameca; Las Canoas, El Chante, Autlán; Tuxcacuesco; Telcampana, near San Gabriel; Sayula; Ciudad Guzmán (Zapotlán); Tuxpan; Tenamaxtlán; Mascota; Talpa; Ayutla; and Teocaltiche. In addition, although we have no samples, informants definitely report sweet corn from: La Huerta, Purificación; Zapotitlán; El Jazmín; San Pedro Tlaquepaque; Jalostotitlán; San Juan de los Lagos; Lagos de Moreno; and Encarnación.

In Jalisco sweet corn is not a commercial crop and is grown chiefly for home consumption. It is offered for sale only in small quantities and, as far as we know, invariably in the form of confections (see below). It is essentially a product of the *ranchos* and small *pueblos;* if not actually scorned by city people, it is regarded by them as a somewhat rustic food. Ordinarily sweet corn is planted in the *milpas* as a summer *(temporal)* crop, although there is no physical reason why it should not be grown in irrigated plots or in gardens. The feeling seems to be that it is not of sufficient importance to warrant the bother of irrigating.

The cultural data presented below apply primarily to western Jalisco, specifically to the Ameca-Autlán-Tuxcacuesco districts. A few supplementary data suggest that as regards maize utilization western Jalisco may differ somewhat from the Los Altos zone, the great expanse of high-steppe country which extends from Lake Chapala northeastward. From personal observation and from the interrogation of a limited number of informants from diverse parts of the state, the general *maiz dulce* picture appears to be as presented below.

The potential uses of sweet corn are restricted and overlap relatively little with those of the less specialized forms of maize. First and foremost, it must be made clear that *maiz dulce* is not considered satisfactory for *nixtamal* (the dried, mature maize kernel, which is steeped with lime in hot water and when softened is ground on the *metate* to produce the *masa* for making *tortillas*). However, in certain areas (Sayula, Tuxpan, and apparently through much of the Los Altos zone), sweet corn is used for *atole*, a sort of maize gruel.[5] This is not a general practice in western Jalisco.

[5] Several types of *atole* are known in Jalisco, and our data do not specify which of these may be made from sweet corn. Probably it is not the *atole* which has a *nixtamal* base, since it is said specifically that sweet corn is not suitable for the preparation of this near-hominy. Presumably the *atole* in question is made of maize which is boiled (without lime), ground, strained, and served without further ado in a semi-liquid state.

Occasionally, green ears of sweet corn are boiled or roasted, but these are not considered particularly tasty since the maize is gummy and sticks between the teeth. However, in certain areas of Los Altos (Encarnación and Jalostotitlán; *not* in Lagos de Moreno or in San Juan de los Lagos), sweet corn is served as *esquite;*[6] in western Jalisco the latter usually is made with white corn.

Aside from the above-noted uses, which are not general, the culinary functions of *maiz dulce* are pretty effectively confined to two special confections: *pinole* and *ponteduro.*

Pinole[7] is by no means a standard item of diet but is prepared "*por gusto*", when one has a desire for it. Its function is essentially that of a confection. Although of no dietary significance, *pinole* evidently is well established in the local culture, as witnessed by two common proverbs: "No se puede chiflar y comer pinole" (one can't whistle and eat *pinole*) and "El que tiene más saliva come más pinole" (he who has the most saliva eats the most *pinole*). Throughout western Jalisco *pinole* is probably the most common dish made of *maiz dulce.* In the Los Altos zone, specifically in Encarnación and Jalostotitlán, *maiz dulce* similarly is made into *pinole.* However, in two other pueblos of Los Altos (Lagos de Moreno and San Juan de los Lagos), it is said that *pinole* is made exclusively of *maiz negro.* The same is true of the Jalisco-Zacatecas border country (Teocaltiche, Nochistlán), where it is said that sweet corn is too oily for successful *pinole.*

Ponteduro[8] is the second major dish prepared with maiz dulce; it is made throughout Jalisco, wherever sweet corn occurs. A variant of *ponteduro* is known as *pipitoria;* the ingredients are the same but the sweet is shaped into thin, flat cakes instead of balls or separate coated elements.

It should be clear from the foregoing that *maiz dulce* does not play a major role in Jaliscan diet. It is essentially a basic ingredient of several confections which are prepared only occasionally, much as we roast peanuts, pop corn, or make taffy. In afternoon and evening, vendors may appear on the streets or in the plazas of the small pueblos, offering homemade *pinole, ponteduro,* or *pipitoria,* in company with roasted peanuts, toasted *garbanzos, habas,* squash seeds, and similar local delicacies. As far as we know, the commercial aspects of sweet corn are

[6] *Esquite* is prepared from roasting ears which are somewhat old and past their prime. The kernels are cut from the cob and toasted in a clay plate or tray *(comal).* They are then removed to another vessel, sprinkled with salt water, and returned to the hot tray until the moisture has evaporated. They are eaten as a confection.

[7] *Pinole* is prepared from dried, shelled, mature *maiz dulce.* The kernels are toasted in an earthen tray and then ground on the *metate* with *panocha* (known also as *piloncillo,* a coarse brown sugar sold in the form of hard cakes or cones) and *canela* (cinnamon bark or a local substitute therefor). The resulting powder is eaten dry or accompanied by a glass of milk; it does not appeal to an untrained palate, being somewhat reminiscent of licorice powder.

[8] *Ponteduro* is the local equivalent of sugared peanuts or peanut brittle. A syrup of *panocha* and water (sometimes milk) is boiled until it thickens. To it are added the dry, toasted kernels of *maiz dulce,* together with toasted squash *(calabacita)* seeds and roasted peanuts. The mixture is removed from the fire and stirred until it hardens. The *panocha* coats the various elements or, if desired, binds them into a ball. The resultant confection is extremely sweet and because of its hardness is something of a test of dental prowess.

confined to this type of informal vending. In fact, the occurrence of sweet corn in Jalisco is a relatively inconspicuous affair and might well escape the notice of a casual traveler.

SUMMARY

The relative importance of cultural and genetic data in determining the origins of crop plants is discussed briefly. Their comparative significance is very different for sweet corns and dent corns. The various morphological and cytological features of Jaliscan sweet corns are described and summarized. While generally similar to other Jaliscan maize, they are more uniform as a group and have larger, broader ears. They are widely, although not commonly, grown in Jalisco by country people, chiefly for home use in the form of two special confections, *pinole* and *ponteduro*.

The data suggest that sweet corn is not a recent introduction in Jalisco. When similar studies are available for other areas, it should be possible to discuss authoritatively the origins of North American sweet corns.

For assistance of various kinds, the authors are indebted to several members of the staff of the University of California, particularly to Professor Carl Sauer, of the Department of Geography.

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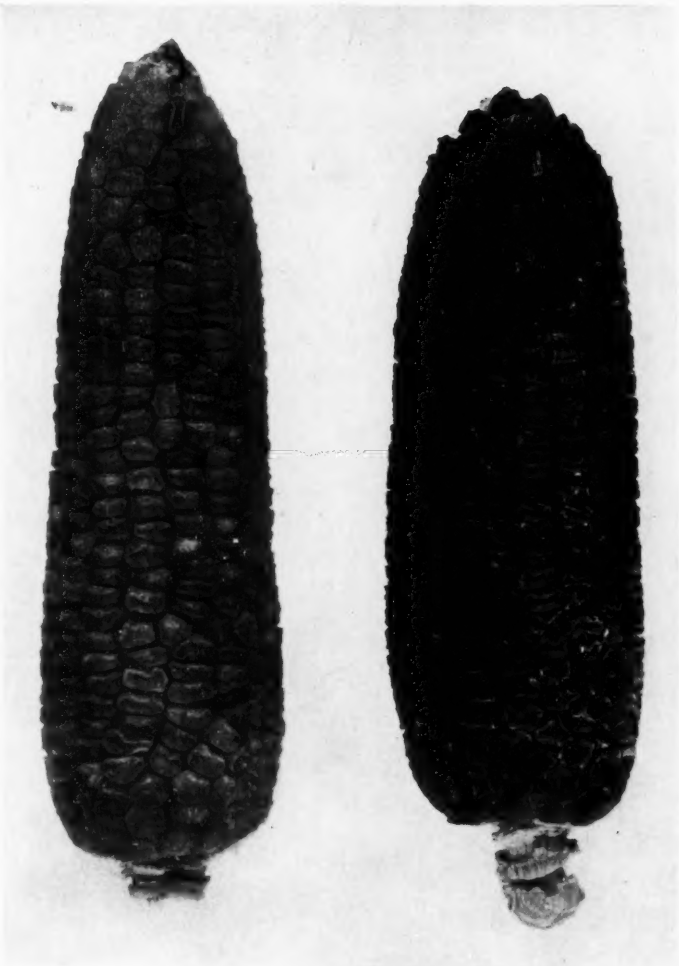
Explanation of Plate

PLATE 4

Two ears of sweet corn from Unión de Tula, Jalisco; x about 9/10.



KELLY & ANDERSON—JALISCAN SWEET CORN

THE MAIZE TRIBUTE OF MOCTEZUMA'S EMPIRE[1]

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The original tribute list of Moctezuma's empire is still in existence[2] and can be consulted in the Salon de Codices of the Museo Nacional de Arqueologia at Mexico City. It is made up of thick pages of so-called maguey paper, bound along one edge into a book, instead of being folded back and forth screen-wise like most native codices. It was primarily a very practical, book-keeping document, and the glyphs were not fantastically elaborated as in more ceremonial codices; they are strong and effective cartoons of the kinds of tribute. Four hundred years have not completely obliterated the simple colors of the original, and the glyphs of the maize plant still show green leaves, yellow tassels, and ears with green or dark red silks. The tribute list is arranged by provinces, a province to a page (see plate 5). The glyphs for the towns are arranged around the lower and outer edges of the page. The tribute due from the province fills up the interior of the page, the various articles being arranged in a more or less standardized fashion, so that maize and beans are in the upper left-hand corner on fifteen of the sixteen pages where they occur. The glyphs, while crudely drawn, are nearly always effective representations of the tribute: jars of honey, mantles of cotton cloth, live eagles, etc., from the top of which protrude the glyphs for number (digits, banners, purses, as the case may be).

The original list has undergone several changes, some of which enhance its value to us. It was annotated in Náhuatl ("Aztec") in early post-conquest times and even more briefly in Spanish at a later date. Unfortunately, these annotations have never been adequately reproduced in any of the "editions" which the manuscript has suffered. About eight pages are now missing, some of them having disappeared since a copy was prepared for the 'Codex Mendocino'.[3] This latter well-known 'Codex' was made up for the Emperor Charles V by an Indian copyist who worked in such haste that he inserted a statement to that effect as an apology to future scholars.[4] The document was designed to tell the emperor something about his new possessions and, along with copies of several pre-conquest documents,

[1] The form Moctezuma will be noted. Though Montezuma (with an 'n') is deeply rooted in English, it is a barbarism.

[2] Matrícula de Tributos, No. 52, Salon de Codices, M. N. de Arque.

[3] In the 18th century Archbishop Lorenzana reproduced the 'Matrícula' (the tribute list) in his edition of Cortes' letters. It was then more complete than to-day. A century ago the United States Ambassador Poinsett (from whom the Poinsettia gets its name) carried off a fragment to Philadelphia, and this has only recently been recovered.

[4] See in this connection an interesting paper by Gómez de Orozco, Rev. Mex. de Etudios Antrop. 5:43-52.

it incorporated some new material. The copy of the tribute list is extensively annotated in Spanish and forms the second part of the 'Codex Mendocino'. That document never reached the Emperor Charles but fell into the hands of French pirates. After a long and adventurous career it came to rest in the Bodleian library at Oxford. It has been published and cited so often as to obscure the importance of the originals on which it is based.

The age of the original tribute list can be approximately set within the last decade of Moctezuma's rule since it includes Tlaxiaco, a town not conquered until 1511[5], among the towns which paid tribute. It therefore gives us an unusually

Fig. 1. The Tlapalizquixochitl Tree

[5] The widespread belief that Tlaxiaco was conquered in 11. Acatl (1503) rests on the mistaken annotation of a picture in the 'Codex Telleriano Remensis'. Actually it was conquered in 1511 or 1512, as will be shown below. It may be argued that Tlaxiaco was subjugated long before, in the middle of the 15th century, and lost, and that it was kept in the tribute list just as the English kept up their claim to Calais. This is more than doubtful. While it is true that the Texcocans made important conquests in the Mixteca in the late 1450's these did not include Tlaxiaco. And, in any case, the presence of the Pacific province of Cihuatlan, conquered by Moctezuma's predecessor, is evidence that the 'Matricula de Tributos' was compiled no earlier than the previous reign, which ended in 1502. Evidence for 1511 or 1512 as the date of Tlaxiaco's conquest is as follows: The year 6. Acatl (1511) is given in Lehmann's edition of the Anales de Quauhtitlan (Mexiko und Colhuacan, verse 1277) and in Chimalpahin, septieme relation. Ixtlilxochitl, I, 258, says the same, the name here being corrupted into Alasquiyauh. In the 'Codex Aubin' and the unpublished 'Codex Mexicanus' (Cf. Boban, pl. 23-24) of Paris 7. Tecpatl (1512) is given. The same time is implied in Torquedmada's story of the event (I, 215), which he places in the 10th or 11th year of Moctezuma II. Moctezuma acceded in 1502, according to the 'Telleriano'. The Mexicans "went against those of Tlachquiauhco" at that time "and destroyed them, leaving nothing in the town, and brought back Malinal, the lord of that province, as prisoner. And all those who were captured in this war were killed" in the dedication of new temples. Altogether, "12,210 persons were sacrificed." This included Malinal, according to Ixtlilxochitl (I,258).

The cause of this campaign was the refusal of Malinal to sell or give Moctezuma a famous flowering tree called *Tlapalizquixochitl*, says Torquemada (I, 196). Of this Sahagun, in his chapter on flowering trees (Lib. XI, Cap. VII, Sect. 10), says: "There are other flowers which are called *Tlapalizquixochitl*, and they are so called not because they are red all over, but because they are spotted and striped with red." Nicholas Leon has identified this plant as no. 685 A of the Paso y Troncoso edition of 'Codex Florentino' plates to Sahagun (see fig. 1).

The question of the date of Tlaxiaco's conquest is resolved, indeed, by the very 'Codex Telleriano', if we disregard the European-added text, and look at the original native picture for the year 6. Acatl (1511). A warrior, dressed for his death in the gladiatorial sacrifice, is shown with the glyph of a ball-court *(tlachtli)* and falling rain *(quiauitl)* which make up the word Tlachquiauhco (Tlaxiaco). There is no reference to this in the Spanish commentray. If Tlaxiaco fell in 6. Acatl (1511)—which all the evidence indicates—what is the meaning of the ball-court-and-rain glyph given under 11. Acatl (1503) in the 'Telleriano'? It is certainly to be read Tlachquiyaucho. The commentator, at a loss, interprets the rain symbol twice and speaks of rain *(quiauitl)* in *Tlachquiauhco* (more exactly, he calls it snow). Now weather was not a favorite topic in these laconic Indian records, where many a monarch got in only by being born and dying. The explanation of the Tlachquiauco glyph in the 'Telleriano' in the year 11. Acatl (1503) may be sought in the 'Historia Tolteca-Chichimeca': "In the year 11. Acatl (1503) Tlachquiauitl, lord of Tepexic, was conquered. He was conquered by the Mexicans". This was because Tlachquiauitl had attacked the chief of Quauhtlatlauhcan. Both of these towns lay within the Mexican province of Tepeacac, and the overlords didn't want their tributaries burning each other's corn-fields. Hence the redundant glyph, so long misread as "Tlachquiauhco" in the 'Telleriano Codex.'

accurate and detailed picture of Moctezuma's empire at the height of its expansion. Barlow's recent[6] identification of the provinces and towns of the tribute list with present and prehistoric Mexican sites makes it possible to plot the distribution of the maize tribute in detail, province by province. In the following list the provinces are given in the order in which they appear in the 'Codex Mendocino' copy, and each province is identified by the town whose glyph initiates the series of towns of the province. Modern names are given in parentheses when they are unlike the ancient names. In a few cases where the page has been divided into sub-provinces the same rule has been followed in selecting the leading towns. A hyphen has been used below in listing these "sub-provinces."

TRIBUTE BY PROVINCES

Tlatelolco	no maize
Petlacalcatl	one crib
Acolhuacan	one crib
Quauhnahuac (Cuernavaca)	one crib
Huaxtepec	one crib
Quauhtitlan	one crib
Axocopan (Ajucuba)	one crib
Atotonilco	one crib
Hueypuchtla	one crib
Atotonilco (el grande)	one crib
Xilotepec	one crib
Quahuacan	one crib
Toluca	two cribs
Ocuilan	one crib
Mallinalco-Xocotitlan	two cribs
Tlachco (Taxco)	one crib
Tepequacuilco	one crib
Cihuatlan	no maize
Tlapan	no maize
Tlalcoçauhtitlan-Quiauhteopan-Yoaltepec	no maize
Chalco	six cribs
Tepeacac (Segura de la frontera)	two cribs
Coayxtlahuacan (Coixtlahuaca)	no maize
Coyolapan (region of Oaxaca City)	two cribs
Tlachquiauco (Tlaxiaco)	no maize
Tochtepec	no maize
Xoconochco (Soconusco)	no maize
Quauhtochco (Huatusco)	no maize
Cuetlaxtlan (Cotastla)	no maize
Tlapacoyan	no maize
Tlatlauhquitepec	no maize
Tuchpan (Tuxpan)	no maize
Atlan	no maize
Ctzicoac	no maize
Oxitipan (Ciudad Valles region)	no maize

The above list raises three special problems: the size of the tribute; the interval of payment; the area of the maize tribute. They will be discussed in that order.

[6] Barlow, R. H. Ibero-Americana. (In press).

1. *The size of the tribute.*—Throughout the tribute list the maize is shown in big square wooden corn cribs or granaries (see pl. 5). The annotator of the 'Codex Mendocino' refers to them in Spanish as "troxes" and says that one troxe holds 4 to 5,000 hanegas[7]. For the next province he says[8] it takes 5,000 hanegas to fill a troxe. Thereafter the size is given by the annotator as being the same as those already described. An hanega (or "fanega" as it is written in modern Spanish) is a notoriously loose term of dry measure. The modern Spanish fanega has been equated to 1.6 English bushels, which would be slightly over 2 American bushels. For Mexico 2.5 American bushels is a conservative equivalent. This would mean that the tribute was paid in units of around 10,000 bushels.[9] This tribute was apparently of shelled corn rather than corn on the cob. The glyph is always a representation of a corn grain rather than an ear of corn and in the original tribute list, corn, beans, *chia (Salvia hispanica)* and *huautli* (Amaranth seed) are usually summarized and represented in the same troxe. Moreover, shelled corn ("en grano") is mentioned in other tribute reckonings (see note 9).

The cribs were apparently large wooden affairs set up off the ground on rocks or posts. The glyph always shows them with a top and a bottom and with a varying number (usually seven) of straight horizontal boards in between. The glyphs are always colored a light red-brown, as if they were wooden. In all but one instance the crib is represented with a door or ventilating hole slightly above the middle. On the original manuscript this door (if such it be) is left uncolored or colored the same as the rest of the crib, or in one instance is painted light gray. There is nothing in the glyph to suggest that it was a crude open crib. It must rather have been some kind of carefully fashioned imperial granary. There is no indication of cracks between the logs or boards and the ends are finished off square. Furthermore, exactly the same kind of glyph is used for the storage cribs for beans and for chia seed which would certainly have required a tight, carefully built structure. From other sources[10] we have a written description of the imperial storehouses at Texcoco. Speaking of the court buildings there, the account goes on to say:

> "To the north of the above mentioned houses and near the kitchens were several granaries (graneros) and bins (troxes) of astonishing magnitude in which the king had a great quantity of maize and other seeds which were kept for the lean years and each of them contained four or five thousand hanegas and they were kept in such order that the air entered on all sides so that the seeds lasted many years".

The usual tribute for a province was one crib of corn, but in several instances two or more were exacted. The total number on the list is 28, which would make the total tribute 28 times 10,000 or in round numbers 300,000 bushels of maize. This number is of course only an approximation, but it does give at least a notion

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[7] "en cada un troxe cabyan quatro y cinco myll hanegas lo qual tributauan una vez en al año." [Cod. Mendocino. *f. 21 R*].

[8] Cod. Mendocino. *f. 22 V.*

[9] In native units the tribute represented 4,000 tlacopintlis. See Anderson & Barlow: Tlalocan 1²:. 1943.

[10] Ixtlilxochitl 2:266.

of the general order of magnitude of the maize tribute. It was certainly in the tens of thousands of bushels, and it might have been in the neighboorhood of a million bushels.

2. *Interval of payment.*—Without exception, the maize tribute is indicated as being paid once a year. Other tribute might be paid at various intervals; twice a year, four times a year, six times a year (as, for instance, the *chian pinole* tribute from Tlatelolco), but the maize in every instance was to come in once a year. This fact may be of some significance in determining the chief maize-growing methods of the empire. In modern Mexico the maize harvest may come at different times of year depending, among other things, upon whether or not it is grown on irrigated land or depends upon the natural rainfall. However, maize of the empire (or at least the kind or kinds used as tribute) was apparently an annual crop.

3. *The area from which the tribute was collected.*—The distribution of the tribute by provinces is shown in fig. 2. It should be remembered that the provin-

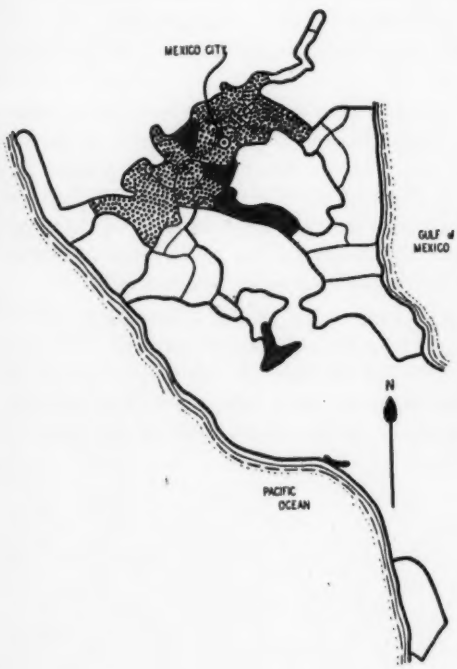

Fig. 2. Map showing the approximate distribution of Moctezuma's empire at the time of the conquest. The heavy line shows the boundary of the empire; the narrow lines are provincial boundaries. Those provinces paying tribute in maize are stippled; heavy stippling represents tribute of more than one crib per province. The authors are indebted to Professor A. L. Kroeber of the University of California for permission to use the original map upon which the figure is based.

cial boundaries as shown in this map are tentative and that a good many details may have to be changed as critical information accumulates. For the purpose at hand, however, it is quite adequate. It will be seen that the maize tribute was very logically distributed. It was levied upon all provinces near the Valley of Mexico and with one exception was not brought from a great distance. For most provinces the tribute was one crib (troxe) of maize, the chief exceptions being the southern end of the Valley of Mexico where the province of Chalco was responsible for five cribs and the Valley of Toluca which contributed two.

The only distant province to pay tribute in maize was that of Coyolapan, which included the region near the present city of Oaxaca. Why it should have been levied upon this province and not from the fertile regions closer to the Valley of Mexico is a puzzle. It is possible that the maize sent from Oaxaca was of a special sort which could not be raised in the cooler climate of the capitol cities. It is also possible that the maize tribute gathered at Oaxaca was not forwarded to the Valley of Mexico though such information as we have been able to find does not bear out this assumption. It is clear from various early Spanish documents that the tribute of this list was independent of, and in addition to, supplies which supported the local garrisons. We know, for instance, that in Totoltepec "they did not give tribute because they formed the frontier with Michoacan and supported the soldiers which they had there, Mexicans, and those of the fortress of Oztoma."[11]

Other documents show that at least a portion of the imperial maize tribute was raised in special fields. "They made a large planting (sementera) all the town together, and what they gathered from this was brought together by these governors and they gave it every year to Moctezuma."[12] The aborigines (Matlatzinca) who remained in one of the border towns after the flight of most of the village when this province was conquered by the Mexicans in the 1470's "made a planting for the lord of Mexico which was 800 brazas long and 400 brazas wide."[13]

Summary.—The tribute list of Moctezuma is described and the tribute in maize is summarized by provinces. The maize tribute was paid once a year and is believed to have been roughly 300,000 bushels. A provisional map of the empire is given showing the distribution of the maize tribute, which for the most part was limited to the provinces closest to the capitol cities in the Valley of Mexico.

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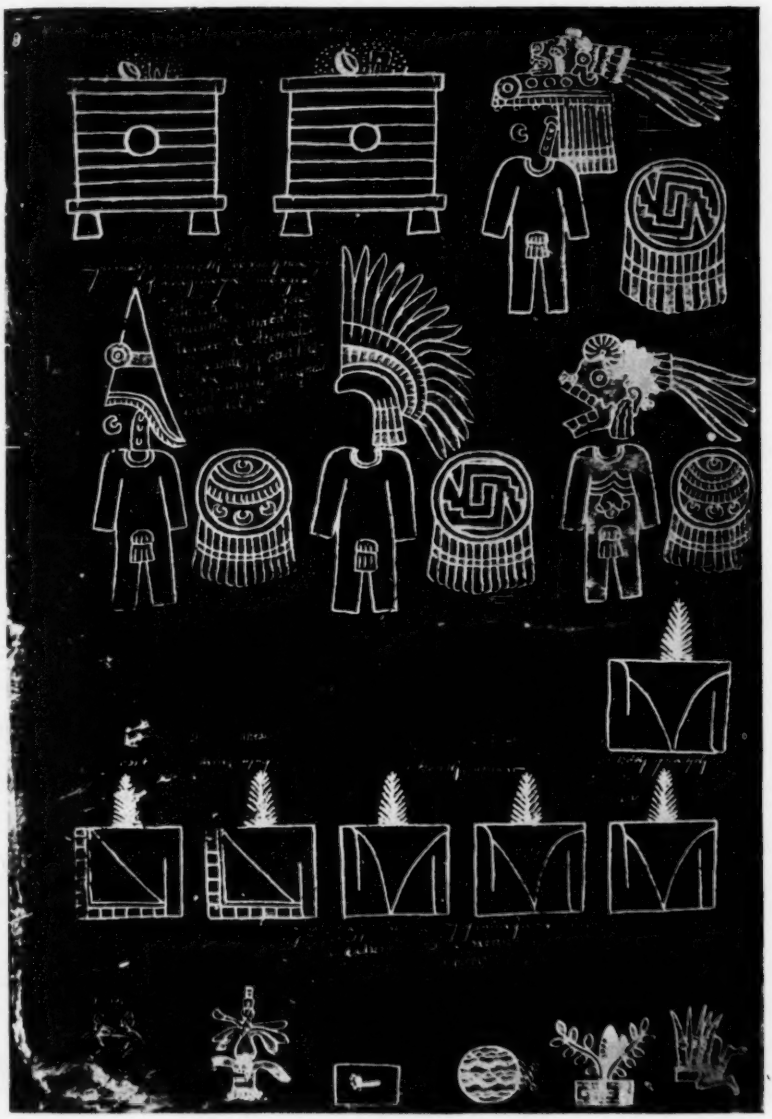
[11] Papeles de Nueva España 6:149.
[12] Epistolario de Nueva España. 6:276.
[13] Zurita. Relación de Texcoco. p. 221.

Explanation of Plate

PLATE 5

Negative photostat copy of the page of the 'Matrícula' devoted to the province of Atotonilco el Grande. The glyphs for the six towns of the province are along the bottom of the page. They are, from left to right, Atotonilco, Acaxochitla, Quachqueçaloyan, Hueyapan, Itzihuiquilocan, and Tulançinco. These place glyphs are like rebuses. The last one, for instance, is made up of the glyph for reeds *(tulan)* and the glyph for little *(çintli,* represented by the nether half of the human body). In the upper left hand corner of the page are the glyphs for cribs *(troxes)*. On top of each crib is the glyph for corn (right) and beans (left). The rest of the tribute of this province consisted of four ceremonial costumes (complete with head-dresses, nose plugs, and shields) and mantles (1600 plain and 800 fancy). The glyph resembling a fern frond which rises from the top of each mantle glyph is the glyph for 400 *(centzontli)*. Immediately below the "troxes" an early scribe has made two brief lines of annotation in Náhuatl. Below this a still later annotator has written six further lines of Spanish.



ANDERSON & BARLOW—MAIZE TRIBUTE

ON THE VASCULAR ANATOMY OF THE CYCADEOID CONE AXIS[1]

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The great fossil cycad beds of the Black Hills in South Dakota and the Freezeout Hills of Wyoming have yielded a tremendously valuable store of knowledge concerning the internal structure of this early and highly specialized group of plants. Nevertheless, a considerable number of questions remain unanswered concerning the Cycadeoids themselves as well as their affinities with other groups. Some of this information will be obtained from further study of the specimens that have long reposed in American museums, and it is hoped that discoveries of new localities will play a still more important part.

It is the purpose of the present contribution to record a fossil cycad locality in the Ferris Mountains of south-central Wyoming and to describe certain imperfectly known features of the vascular anatomy of the *Cycadeoidea* cone axis.

In 1941, when I was collecting fossils in Wyoming, the Ferris Mountain locality was brought to my attention by Mr. W. A. Brox, a geologist and mineral dealer of Rawlins. He showed me a number of silicified cycad fragments in his collection which had been found in those mountains by Mr. Charles Johnson, of Bairoil. Through the generous aid of these two gentlemen a visit to the site was made possible. Only a few supplementary fragments were obtained at that time but these were sufficient to indicate the origin of the specimens. The locality, which was discovered by Mr. Johnson, lies near the west end of the Ferris Mountain range, approximately 10 miles northeast of Bairoil, Wyoming. The fossils had apparently weathered out of the upper Jurassic Morrison formation, in all probability occupying the same or nearly the same horizon as the fossil cycads from the Freezeout Hills, some 50 miles to the east.

Of the specimens obtained from Mr. Brox and from Mr. Johnson, one consists of the apical portion of a columnar trunk. Prior to sectioning for study it was 12.5 cm. long and nearly 15 cm. in diameter. That it is the tip of a trunk or branch is clearly indicated by the rapidly tapering form of the xylary "cylinder" and the dense aggregation of the leaf bases composing the upper surface. The trunk fragment was cut transversely into four sections, and while a study of the exposed surfaces revealed no exceptional features not already known in Cycadeoidean anatomy a number of cone axes was noted. In view of the excellent preservation and the highly gratifying quality of the peels obtained it seemed probable that serial preparations would reveal significant information pertaining to the stem-peduncle xylem transition.

[1] Issued November 20, 1943.

General Anatomy.—

As is usual in the genus *Cycadeoidea*, the pith is large, measuring 4 cm. in diameter, and it is liberally supplied with irregular, and probably secretory, sacs. These are found both in the cortex and leaf bases and are also filled with a dense brown substance throughout.

The stele consists of a cylinder 6–8 mm. thick (radially) which is frequently segmented by the departure of leaf and cone traces. Xylem and phloem are present in approximately equal quantities and are readily distinguished in transverse and radial sections. The tracheids are predominantly scalariform (fig. 9), and there is no evidence of distinct annular growth in transverse section, the wood presenting the aspect of a single uniform ring.

Where the xylem is undisturbed by departing appendage traces the wood rays are generally uniseriate and of considerable height. A few have been observed only 3–4 cells high but the majority are 15 or more cells high. Not infrequently they tend to be biseriate in the central portion. The ray cell size is very variable, ranging from 105 μ high by 48 μ broad (tangential) to 24 μ x 12 μ.

The Stem-Peduncle Stele Transition.—

In Wieland's monumental treatment[2] of the American petrified cycadean trunks he gives an account of the anatomy of the lower portion of the peduncle stele of *Cycadeoidea Wielandi* Ward. The equipment available at the time rendered impossible the preparation of serial sections, and it is to Wieland's credit that he was able to shed as much light on the stem-peduncle stele transition as he did. However, as he indicates in his summary (p. 73), the description that he was able to present is incomplete and difficult to follow. In view of the seemingly significant and distinctive nature of the peduncle anatomy it seems appropriate to quote his summary:

> The general conclusion is that the peduncular bundle is formed from the union of several different bundle strands in the lower part of its course through the cortex, and that these strands consist primarily of a main branch arising directly from the woody cylinder, which may, however, be connected with either lateral or subtending leaf traces. The leaf traces appear in general to arise from the woody cylinder as horseshoe bundles, with the phloem outside, these bundles soon assuming a more or less brokenly-circular form in the most of their course through the cortex before dividing up in the leaf base.

As a generality, this summary is quite correct although there are many gaps in the description which render it, according to Wieland himself, "unexpected . . . . difficult to explain." In the following paragraphs I shall present a detailed account of the stelar anatomy of the peduncle from its origin in the stem stele to its departure from the trunk as a free appendage.

In following the transition from below upwards the first indication of the departure of a peduncle stelar system presents itself in the form of three arcs of xylem about 4 mm. apart (fig. 1). Of these, the two laterals (*a*, *b*), which are markedly more elongate radially than ordinary leaf traces, depart rather abruptly from the stele while the central trace (*c*), as may be noted in the succeeding photographs, passes out into the cortex much more slowly.

[2] Wieland, G. R. American fossil cycads. Carnegie Inst. Washington Publ. 34[1]. 1906.

Soon after their departure from the stem stele each of the two lateral traces closes to form a radially elongate stele. Almost immediately these become centrally constricted, foreshadowing their rapid division into two more or less equal parts. In fig. 2 it is clear that the two pairs of arcs, a_1, a_2 and b_1, b_2, have resulted from the respective divisions of *a* and *b* in fig. 1. The preservation in the region of the *b* lateral is rather faulty, which accounts for the light streak through the photograph. Aside, however, from some slight size differences, the system is bilaterally symmetrical and consequently we may center the discussion around the more perfectly preserved *a* lateral.

Next the a_2 and b_2 segments of the two laterals pass directly out, each into a petiole base. The further division of these traces in the petioles involves no features that are not already known in Cycadean anatomy and need not be considered further. Now the inner segments of the laterals (a_1, b_1) close in, resulting in two nearly cylindrical steles. These pass to a position closely flanking the now radially extended central trace (fig. 3), open directly toward it, and the three fuse, resulting in a short cross-shaped figure (fig. 4)[3]. This appendage system, which is still connected with the stem stele, is then pinched off (fig. 5) from the latter and tends to take the shape of an ellipse. One more departure is, however, in the order of things. The outer portion (c_1) of the original central trace *c* passes out (fig. 6) into a petiole which directly subtends the peduncle. The stele of the latter then departs from the cortex without further additions or losses. The entire transition from fig. 1 to fig. 6 extends through a vertical distance of 12 mm.

A number of other peduncle steles have been followed through parts of their lower course, sufficient to establish the above description as typical. It seems very likely, moreover, from a comparison with Wieland's figures[4] that essentially the same structural relationships prevail in *Cycadeoidea Wielandi* Ward. Beyond this, a generalization is speculative but in view of the rather close comparison in other anatomical details between *C. Wielandi* and my own specimen with numerous other species of *Cycadeoidea* it seems safe to predict that the transition described here will be found to be typical for most of the closely related species.

Taxonomy.—

If one looks at all carefully into the literature relating to petrified cycadean stems it soon becomes clear that a majority of the specific names are quite meaningless as biologic entities. It seems to have become standard practice to assign a new specific name to each newly discovered specimen. However, it is not as difficult as might be expected to condone this custom despite the abundance of names that results. The fact remains that one rarely encounters paleobotanical specimens that present greater difficulty in their preparation of study material.

[3] One of the initial saw cuts was made near that portion of the block shown in fig. 4. Thus in order to survey the course of the peduncle stele it was necessary to prepare peels from both of the adjoining surfaces. Consequently figs. 4, 5, and 6 are reversed, lateral *b* appearing at the left instead of the right as in the preceding fig. 3. It seemed best to illustrate the series this way since somewhat inferior prints were obtained when the negatives of either half of the series were reversed.

[4] Wieland, op. cit. pp. 69-71.

This, coupled with the hesitancy on the part of many investigators to dissect specimens of museum-display quality, has resulted in the description of a great many specimens concerning which little or nothing of importance is known. Ward's descriptions, based almost exclusively on external characters, are very nearly worthless. Until the internal structure of those species is investigated the names remain only as catalogue numbers. Even in Wieland's informative and beautifully executed volumes I personally find it difficult to single out distinctive characters for very many of the numerous species that are recorded.

This is perhaps a weak excuse to carry on a weak and incomplete system. Nevertheless, the Cycadeoid described here might be "tentatively assigned" to a number of recorded species, one, all or none of which choices might be correct. In view of this uncertainty it seems that less ultimate confusion will arise if it is recorded, for the present, as a distinct taxonomic entity.

Cycadeoidea Broxiana Andrews, n. sp.

Species based on the apical portion of a columnar type trunk; pith 4 cm. in diameter, containing abundant secretory sacs, the latter also found in cortex and petioles; stele a single cylinder 6–8 mm. thick, xylem and phloem quantitatively equal, tracheids scalariform, rays uniseriate, occasionally biseriate, cells very variable in size; ramentum abundant about bases of petioles and peduncles; leaf trace branches about 20, ventral ones turned strongly inward; periderm well developed in cortex of peduncle and peduncular bracts. Type specimen *(#1463)* deposited in the collections of the Henry Shaw School of Botany, Washington University, St. Louis.

Acknowledgment.—

I wish to express my sincere appreciation to Mr. W. A. Brox, of Rawlins, Wyoming, for valuable aid in the field and his unselfish gift of botanical specimens of scientific value.

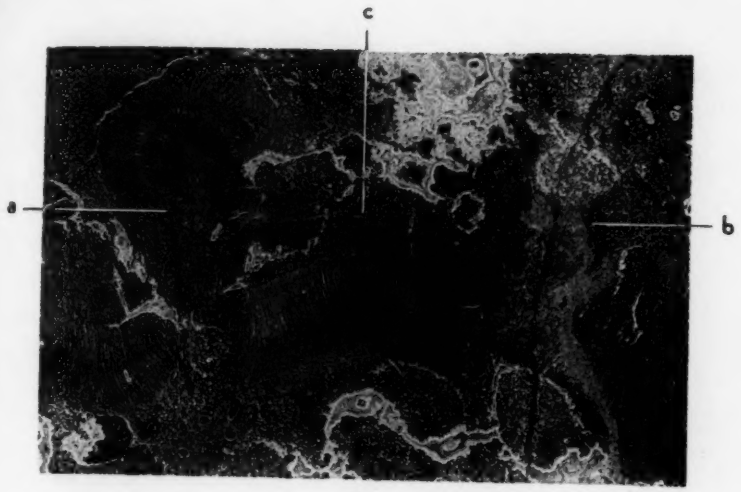
Explanation of Plate

PLATE 6

Cycadeoidea Broxiana

Fig. 1. Transverse section through stem stele showing origin of peduncular traces; *a*, *b*, lateral traces, and *c* central trace. 1463C-a, t27; x 5.

Fig. 2. Same at a higher level showing division of the lateral traces. The traces, a_1, a_2 and b_1, b_2 have resulted from the tangential divisions of *a* and *b* (fig. 1) respectively. 1463C-a, t17; x 5.



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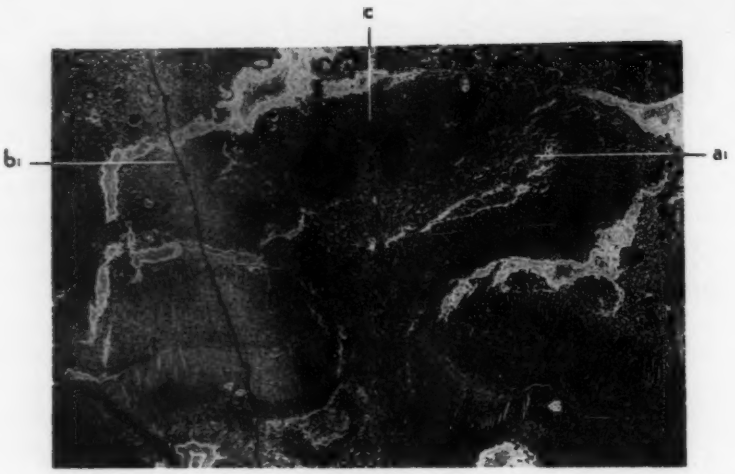
ANDREWS—THE CYCADEOID CONE AXIS



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ANDREWS—THE CYCADEOID CONE AXIS

Explanation of Plate

PLATE 7

Cycadeoides Broxiana

Fig. 3. The laterals a_1 and b_2 have closed and are about to fuse with the now elongated central trace. 1463C-a, t8; x 5.

Fig. 4. Showing fused lateral and central traces. 1463B-B1; x 5.

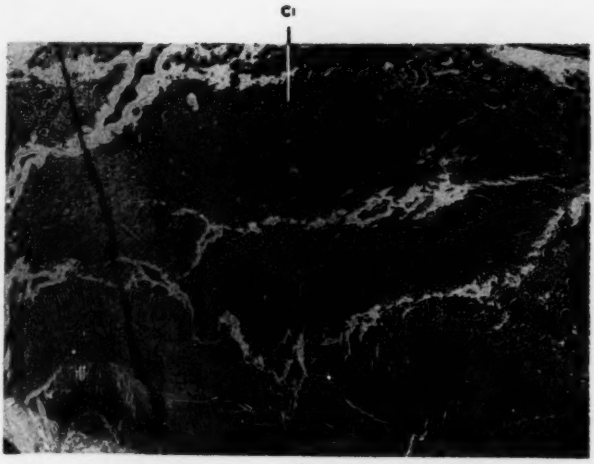
Explanation of Plate

PLATE 8

Cycadeoidea Broxiana

Fig. 5. Showing departure of peduncular stele from stem stele. 1463B-a, b12; x 5.

Fig. 6. Showing departure of trace from peduncle stele into subtending petiole. 1463B-a, b27; x 5.



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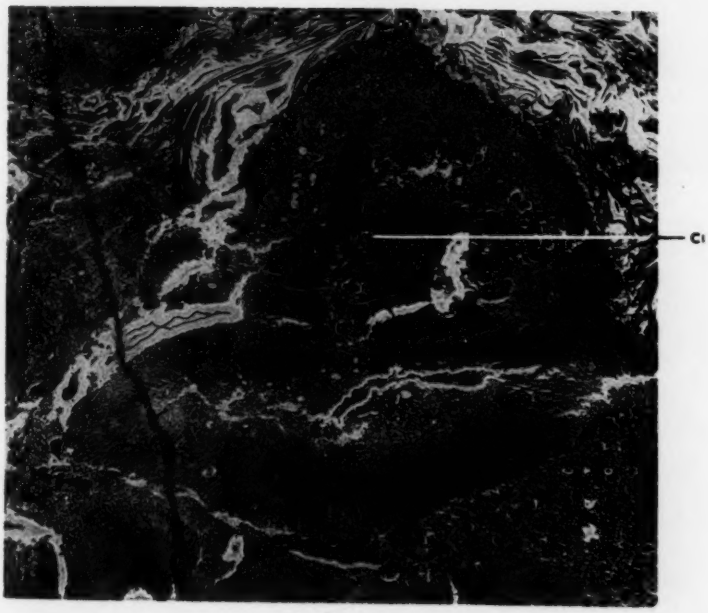

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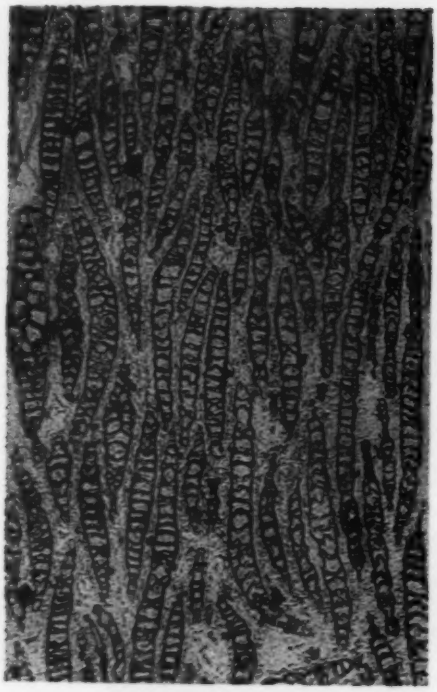
ANDREWS—THE CYCADEOID CONE AXIS



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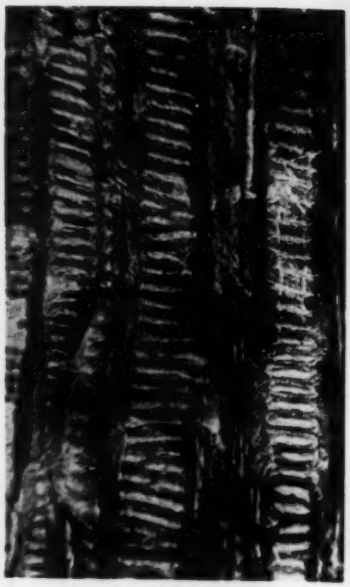

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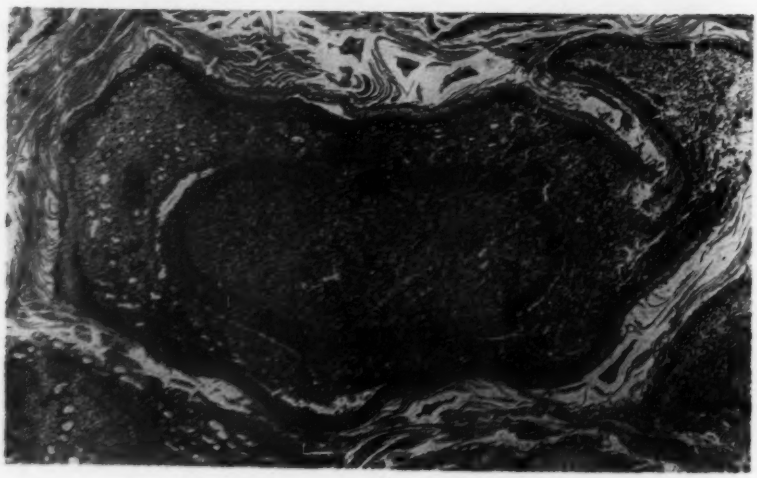

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ANDREWS—THE CYCADEOID CONE AXIS

Explanation of Plate

PLATE 9

Cycadeoidea Broxiana

Fig. 7. Cross section through base of peduncle. 1463A-A, b15; x 5.

Fig. 8. Cross section through ramental scales. 1463A-A, b2; x 80.

Fig. 9. Radial longitudinal section through stem wood showing scalariform pitting of tracheids. 1463D-b, s1; x 380.

CONTRIBUTIONS TO OUR KNOWLEDGE OF AMERICAN CARBONIFEROUS FLORAS[1]

VI. Certain Filicinean Fructifications

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Carboniferous plants collected from the roof shales of American coal mines received comprehensive treatment at the hands of paleobotanists of a half century ago, the better known and basic contributions being those of Lesquereux ('80-'84) and White ('99). However, in view of our increased knowledge of the floras that these men dealt with, as well as the recent innovations in the technique of handling compression fossils, extensive revisions in the literature are necessary. Furthermore, modern methods now render very valuable the comparatively small, scattered, and fragmentary specimens of fertile fronds that apparently had been discarded in favor of the larger and more attractive museum-type of specimen. In most cases these were sterile and in themselves of little biological value.

During the past year I have obtained, largely through the kind offices of Mr. John Jones, Safety Superintendent of the Old Ben Mines, in Franklin County, Illinois, a number of interesting specimens bearing filicinean fructifications. The specimens are not numerous, and generally only small portions of the entire frond are present. They do, however, display characters pertaining to the morphology of spores and sporangia, characters that are considered to be of prime importance in the diagnosis of living forms. Although our investigations thus far must be considered as only an introduction to more extensive and critical studies, it seems advisable to present the results to date in view of current war-time regulations which prevent further collecting in the shaft mines.

All of the specimens described in the following pages were obtained from the roof shales of the Old Ben Mine No. 11. These shales overlie coal No. 6 and constitute the basal member of the McLeansboro formation (upper Allegheny), being of upper-middle Pennsylvanian age.

SCHIZAEACEAE

Senftenbergia Corda. 1867.

This genus has come into prominence recently by Radforth's ('38-'39) demonstrations that *Dactylotheca* Zeiller is founded on a misconception and that forms previously assigned to it must be referred to *Senftenbergia* or *Asterotheca* (Radforth, '42). Furthermore, it has been shown that *Senftenbergia*, so far as its critical characters are concerned, belongs emphatically in the Schizaeaceae. Specimens of the type that Kidston believed referable to *Dactylotheca* have long been

[1] Issued November 20, 1943.

known in America, but modern technique has now confirmed Radforth's conclusions from American material in striking fashion. The material studied was obtained in association with fronds of *Pecopteris plumosa* var. *dentata*, discussed below, and strongly suggests that the characters exemplified by the *Senftenbergia* pinnae are correlative with these sterile fronds.

Technique.—

The technique employed was essentially the same as that described by Radforth in the above-cited papers, and by Andrews and Pearsall ('41) for carbonaceous compressions of a Cretaceous *Anemia*. Only one well-preserved specimen was available, and, in order to obtain sufficient sporangia without affecting the specimen, small portions, about 1 cm. square, were removed with needles, the fossil side coated with a nitrocellulose solution and immersed in dilute hydrofluoric acid overnight (very small fragments were placed in the acid directly). When the shale-free sporangia were then placed in the oxidizing fluid (nitric acid and potassium chlorate), followed by washing in dilute ammonia water, their walls gradually cleared, revealing the contained spores. Three to four hours were sufficient, in most cases, to bring about the almost complete disintegration of the sporangium wall, isolating the spores as a unit mass (figs. 7, 8). The material thus prepared was mounted in "crystal white" Karo.

Senftenbergia plumosa (Artis) Radforth var. **Jonesi** Andrews, n. var.

Judging from the two pinnae composing the specimen (fig. 1) they are parts of a comparatively large frond, and the size attained by the supposed sterile frond (or portion thereof) supports this assumption. Almost the entire under-surface of the secondary pinnae appears densely clothed with sporangia (figs. 2, 3) which are attached by a short stalk (figs. 4, 5). The mature ones that have shed their spores exhibit but little variation in size, averaging .52 x .26 mm. The annulus is distinctly Schizaeaceous, consisting of a nearly apical ring of two rows of longitudinally elongate and irregularly interlocking cells (figs. 5, 17). It is difficult to locate specimens which display the apical plate in end view, since the great majority of the sporangia have been laterally compressed in fossilization. Figure 16 shows the distal end of a sporangium, from which it seems clear that the apical plate consists of a number of cells, comparing closely with the apical plate of living *Anemia* species.

Many of the sporangia still retain their spores. The less mature spores are smooth-walled and adhere together tenaciously in a more or less ovoid mass, although tapering somewhat toward the proximal end (fig. 8). The mature spores (fig. 9) are approximately 50 μ in diameter and are characterized by irregular ridges and stout spines which may be forked at their tips.

During the course of treatment in the oxidizing fluid one sporangium was observed in which the spores were almost mature judging from their sculpturing,

yet still retained together in a unit mass after dissolving the sporangium wall. Most of the spores were readily separated with a needle, and the number determined was approximately 118. That the spore mass represents the entire contents of a sporangium was evinced by its uniform shape conforming to that of the sporangium as a whole prior to treatment.

It is not possible to discern distinctly a lamina in the fertile pinnae but that such was present seems evident from the abundance of epidermal hairs that clothe not only the pinna rachis (fig. 15) but the secondary pinnae as well. The hairs and sporangia cover a sufficiently wide area as to leave no reasonable doubt that a lamina was present although it may have been somewhat narrower than the sterile foliage.

The hairs vary somewhat in size, are branched (figs. 6, 17), and display irregularly thickened cross-walls. The technique involved in handling such delicate structures was necessarily specialized and is perhaps worth a separate notation. A portion of the specimen was dipped in 20 per cent hydrofluoric acid for about one minute. This cleared the dark gray shale to a much lighter shade and tended not only to partially liberate the sporangia and hairs from the matrix but, due to the increased color contrast, greatly enhanced study and photography. Hairs were then carefully removed with needles and placed in the oxidizing fluid for about three minutes. After washing and treatment with ammonia water the larger branched ones appear as shown in fig. 17. If the oxidation time is prolonged the hairs become nearly colorless and so fragile as to be exceedingly difficult to manipulate.

Discussion.—

Of the European species of *Senftenbergia* described by Radforth our specimen agrees very closely with S. *plumosa*. The general appearance of the sporangia and their contents is almost identical in the two and they compare very closely in size as shown in table 1.

TABLE I

A DIMENSIONAL COMPARISON OF THE SPORANGIA AND SPORES OF *S. PLUMOSA* AND *S. PLUMOSA* VAR. *JONESI*

	Sporangium length (mm.)	Sporangium width (mm.)	Spores per sporangium	Spore diameter (μ)
Senftenbergia plumosa (Artis) Radforth	.54	.27	200	50
S. *plumosa* (Artis) Rad. var. *Jonesi*	.52	.26	118	50

It may be seen that there is no appreciable difference in sporangium or spore size although a discrepancy appears in the reported number of spores per sporangium. I am inclined to believe that Radforth's number, which is based on calculation, is high in view of the fact that the one given here is based on an actual count and the spores and sporangia of both agree very closely in size. The structure of the annulus and spore exine sculpturing also compare very closely

(cf. Radforth, '38, pl. II, fig. 6). Radforth's figures do, however, seem to display a more prominent lamina than the Illinois specimen, although this may be due simply to poorer preservation in the latter. Because of that difference, as well as the variation in reported spore output and certain variable characters relating to the supposed sterile foliage, it seems advisable to designate the specimen described here as a distinct taxonomic entity.

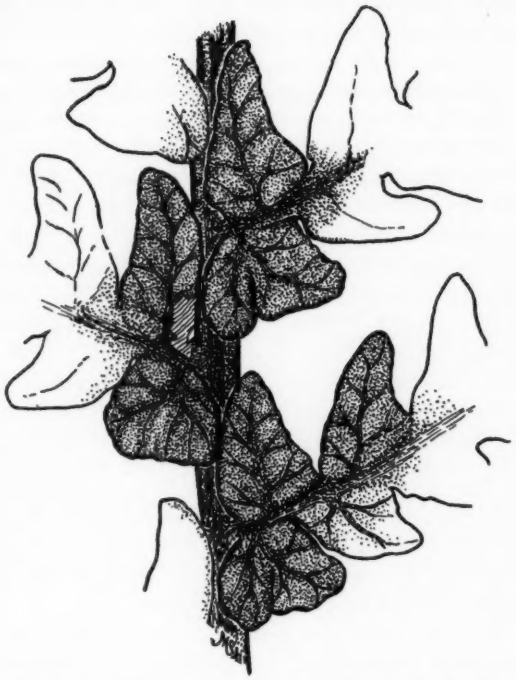
STERILE MATERIAL

Pecopteris plumosa var. **dentata** (Bgt.) White.

We have found associated with the above-described fertile material numerous specimens of a Pecopterid-type frond. In view of our knowledge of the foliage of other species of *Senftenbergia*, as well as certain characters exemplified by S. *plumosa* var. *Jonesi* which are correlative with this particular *Pecopteris*, this will be considered in some detail.

This plant and its close relatives have been described many times and there is little occasion to repeat the descriptions. Although the outline of the large fronds may have been lance-shaped, it nevertheless seems inappropriate to describe a highly pinnatifid leaf of this sort as "lanceolate." Part of Kidston's ('24, p. 385) description of fronds which he referred to *Dactylotheca plumosa* applies very well to our specimens. "The pinnules on the middle ultimate pinnae are oval-triangular or broadly lanceolate (in general outline) with rounded apices, and united by the whole width of their base to the rachis. The basal inferior pinnule is deltoid-rounded, generally smaller than the others, and occupies the angle formed by the insertion of the pinna on its parent rachis, and frequently has a distinct lobe; the superior basal pinnule is oval or oval-oblong, obtuse, and is almost invariably the largest pinnule on the pinna. The uppermost pinnules become gradually more united to each other and form a more or less lobed, and finally an entire blunt apex to the pinna." Bell ('38, p. 76) also mentions "the punctate rachides of primary pinnae," . . . "the contiguous, smooth-surfaced pinnules which have convex, upper surfaces and a tongue-shaped or subtriangular form. The apparently pointed apices of the pinnules in some specimens have resulted from inrolling of the margins, . . ." This last feature is particularly noted in transfer preparations of the Old Ben material; the infolding may ostensibly shorten the distal inferior pinnule margins in unprepared material by more than half a millimeter and serve to give them a notably triangular aspect so that some of the pinnae appear rather sharply serrate as shown in fig. 13. The venation and form of the basal pinnules are shown in text-fig. 1.

The specimens at hand are notably larger than those described from the Barnsley horizon. The one illustrated in fig. 14, at reduced size, is the most delicate yet seen in the Old Ben material, and it appears significantly more robust than Kidston's Yorkian forms. In a recent collection we obtained a particularly fine and large frond fragment. Judging from the size of the primary pinnae, the



Text-fig. 1. Venation and shape of superior and inferior basal pinnules of *Pecopteris plumosa* var. *dentata*. x 5.

longest of which measures 37 cm., it is safe to say that the frond attained a length of between 1 and 2 meters.

Nearly all of our material is well preserved as coalified compressions. All the veins are sunken on the upper surface which is almost invariably exposed. When portions of the upper side of the lamina do remain attached to the rock the counterpart is apt to still carry a skeleton of the veins distinctly impressed. Thus the veins of pinnules are shallow grooves in the upper surface and prominences of the lower surface. The primary and secondary rachides show a number of irregularly spaced papillose protuberances which no doubt represent enlarged and sclerified hair bases. These are on both upper and lower surfaces of the primary rachis but seem more limited to the lower surface of the secondary branches; the tertiary rachides do not show them clearly, partly because the basal pinnules overlap the rachis (cf. text-fig. 1) and probably also because the emergences on this part of the frond are more delicate. On the secondary rachides the hairs are by no means as numerous as shown by Radforth ('38, p. 1, fig. 1) on a Barnsley specimen.

Cuticular preparations have been made from median pinnae similar to those shown in fig. 13, and from this same specimen. The structure varies dorsally and ventrally and in relation to the veins. Over the veins on the upper surface the cuticle is thin and in maceration frequently splits apart along them. The fragment shown in fig. 11 represents the upper cuticle between the bifurcate tips of one of the lateral veins. Although the central cells tend to be isodiametric, pentagonal or hexagonal, many are elongated. The largest are about 40 x 70 μ in diameter; more isodiametric cells measure about 35 μ. The central elongate cells show no special orientation but toward the veins their long axes parallel the nervation and over the veinlets the cells are still narrower. Due to the delicacy of the cuticle these cell markings are shown indistinctly. Other cuticular fragments show that the veins extend to the margin of the lamina which may be very slightly indented. The cuticle is thicker at the margin, tending to show very elongate rugose markings as may be seen in fig. 10, which represents the ventral and dorsal cuticles connected at the leaf margin and spread out in a single plane. The lower cuticle is much thinner than that covering the upper surface. The cells are elongate, roughly rectangular, and tend obliquely from the margin as shown in figs. 10 and 12. The largest cells are about 30 x 80 μ, the smallest ones 20 x 40 μ. Triangular cells are seen where the oblique lower pattern merges with that of the margin. Neither stomates nor hairs have been observed on these cuticles. Presumably the stomatal areas are on the lower surface where the cuticle is thinnest and least readily obtained by maceration procedure.

It is difficult to compare these data with those given by Radforth for the sterile fronds he has identified with *Senftenbergia plumosa*. The small cuticular fragment he has figured (pl. 1, fig. 3) shows elongate, truncate-lenticular cells averaging about 45 x 15 μ, and what appears to be a hair base. It seems clear that his specimens are easily distinguishable from those described here. This lends further support for the taxonomic distinction of our material, at least in so far as the sterile specimens are concerned, from the older more delicate Yorkian forms.

The differences between our material, identified as variety *dentata* (Bgt.) White, and that which Kidston and Radforth have shown for the Yorkian *Pecopteris plumosa* may be summarized as follows: in var. *dentata:*

1. Fronds more robust.
2. Rachides more sparsely hirsute.
3. Lower cuticles show a somewhat different type of cell pattern.

MARATTIACEAE

Scolecopteris Zenker. 1837.

This genus is based on elongate, stalked synangia composed of 3–5 exannulate sporangia. Certain workers have expressed the opinion that *Scolecopteris*, *Asterotheca* and associated genera may be Pteridosperm micro-sporangiate fructifications. I am inclined, however, to accept the more universally prevalent view that

they are of Marattiaceous affinities. A more detailed consideration of the taxonomy of the group follows on a later page.

Scolecopteris Radforthii Andrews, n. sp.

Pinnules 1½ times as long as broad; pinnule vein branches once dichotomous; synangia of 3–4 sporangia, in two rows, on vein terminations, near margin of pinnule; spore masses 550 μ long, 165 μ broad; spores 32 μ in diameter, calculated number 900 per sporangium. The species is named for Dr. N. W. Radforth in recognition of his contributions to our knowledge of Carboniferous ferns.

Although this species is based on a small fragment of a frond bearing parts of ten ultimate pinnae the spore-bearing organs are well preserved, and there is no reason to doubt that it is a representative portion of a fertile frond. The sterile foliage is not known. The pinnules are about 1½ times as long as broad and ascending (fig. 20). The vein which passes out from the pinna rachis gives off side branches of which the proximal ones dichotomize once while those near the tip of the pinnule may remain unbranched (fig. 18).

The spore-bearing organs consist of synangia borne in two rows near the margin of the pinnules, each synangium being at the terminus of a vein.

Following oxidation treatment the cleared sporangial walls reveal the spore masses within (figs. 21, 22). Each synangium is composed of 3–4 partially united sporangia. The spore masses themselves are distinct in most cases and average 550 μ long by 165 μ broad. There is some variation, however, in the degree of the union of the sporangia into a synangium. One of the synangia was isolated in which the spore masses were united through the greater part of their length and others have been observed in which the basal part of the spore masses seems to have been fused. These instances are exceptional and perhaps due in part to maceration of the sporangium wall, for in most cases the sporangia tend to become isolated as distinct unit masses of spores.

Dehiscence is by means of a longitudinal slit extending the length of the inner side of the sporangium. The sporangia composing a synangium are apparently rather loosely held together and in most cases split apart at maturity.

The spores, such as those shown in figs. 21, 22 and apparently immature, measure 32 μ in diameter, are smooth-walled, spherical, and display a tri-radiate commissure. A few have been observed bearing slender unbranched spines, but completely mature ones have not been found. According to the method given by Radforth ('39, p. 746), the spore output of each sporangium would be calculated as 1090. The sporangia vary in length from 500 to 700 μ but most are approximately 550 μ. Since these measurements pertain to the isolated spore masses which filled a sporangium and do not include the wall, the size of the whole sporangia would have been appreciably greater. The specimen illustrated in fig. 22 may be taken as a typical example. The fact that the sporangia taper at their distal end would make their total volume somewhat less than that of an ellipsoid (the geometric figure assumed in the above-noted calculation) of the same minor and major

axes. Taking this into account an estimate of 900 spores per sporangium may be considered as reasonably accurate. Thus, each synangium produced some 2700 to 3600 spores depending on whether it consisted of three or four sporangia.

The rather crowded nature of the sporangia and the compression that they have undergone make it difficult to portray their organization clearly in a photograph. Consequently, the restorations shown in figs. 23 and 24 have been prepared to present their probable appearance before and after dehiscence in life.

Discussion.—

It becomes increasingly evident that the Marattiaceae, or at least plants bearing Marattiaceous fructifications, were abundant in species as well as numbers of plants in the Carboniferous forests. Of the spore-bearing organs that have been referred to this family the two genera *Scolecopteris* and *Asterotheca* are among the better known, and considerable controversy has arisen as to whether *Scolecopteris* deserves generic rank or whether the species assigned to it should be included within *Asterotheca*.

In his "Handbuch" Hirmer ('27, p. 576) considers *Scolecopteris* as synonymous with *Asterotheca*, and Radforth ('42), in his discussion of *A. parallela*, proffers the same opinion. The present writer feels that this course places entirely too wide a range of spore-bearing structures within a single genus. If one compares typical *Asterotheca* fructifications such as those illustrated by Hirmer (p. 582) for *A. truncata* with species such as Radforth's *A. parallela* ('42, pl. 1, fig. 3), it will be noted that the synangia of the latter appear more or less cylindrical and elongate as compared with the usually flattened disc-like shape of *Asterotheca*.

The macerated synangia of *Scolecopteris Radforthii* (figs. 21, 22) are rather closely comparable with Radforth's figure ('42, pl. 1, fig. 5) of the corresponding structures of *A. parallela;* so similar in fact as to leave little doubt that the two are congeneric. The gross organization of the synangia (figs. 19, 20) is, however, certainly not correlative with *Asterotheca*. The synangia of *A. parallela* and *S. Radforthii* are elongate and stalked, which accounts for their less orderly arrangement in the compressions, especially of the latter. The objection may be raised that the appearance of "typical" *Asterotheca* fructifications is due to compression. It is extremely improbable, however, unless they were naturally short and disc-shaped, that such regularity would result in the fossil state. The restoration of *S. Radforthii* shows the probable appearance of the fertile pinnules in life. Synangia such as these, upon compression, lie more or less flat (longitudinally) against the lamina and so lose in fossilization their characteristic habit. A typical *Asterotheca* presents a radially symmetrical compression indicating a synangium with a comparatively much shorter long axis.

It should be emphasized that I do not in any way criticize Radforth's removal of *A. parallela* from *Dactylotheca* nor his masterly demonstration of the true morphology of the spore-bearing organs. I do feel, however, that the course fol-

lowed by that writer and by Hirmer lends excessive flexibility to the concept of *Asterotheca*.

Acknowledgment.—

The investigations reported here have been made possible chiefly through the generous cooperation of Mr. John E. Jones. I am deeply grateful for his continued support and enthusiastic interest in our studies. To the other employees of the Old Ben Coal Corporation who have extended aid I wish to extend sincere thanks.

My collecting trips to the Old Ben Mine have all been in company with Dr. James M. Schopf, now of the United States Bureau of Mines, and to him is due a very large share of the credit for such results as have been obtained thus far. The fine cuticle preparations illustrated on pl. 11, as well as the text-figure, were prepared by Dr. Schopf, and I am indebted to him for a considerable portion of the description of the sterile *Pecopteris* foliage. It should be noted, however, that the author assumes all responsibility for any of the theoretical views presented.

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Explanation of Plate

PLATE 10

Senftenbergia plumosa (Artis) Radforth var. *Jonesi* Andrews

Fig. 1. Photograph of the entire specimen; x 7.

Fig. 2. A portion of one of the pinnae magnified to show the abundance of sporangia; x 11.

Fig. 3. A portion of a pinnule showing the marginal position of the sporangia; x 20.

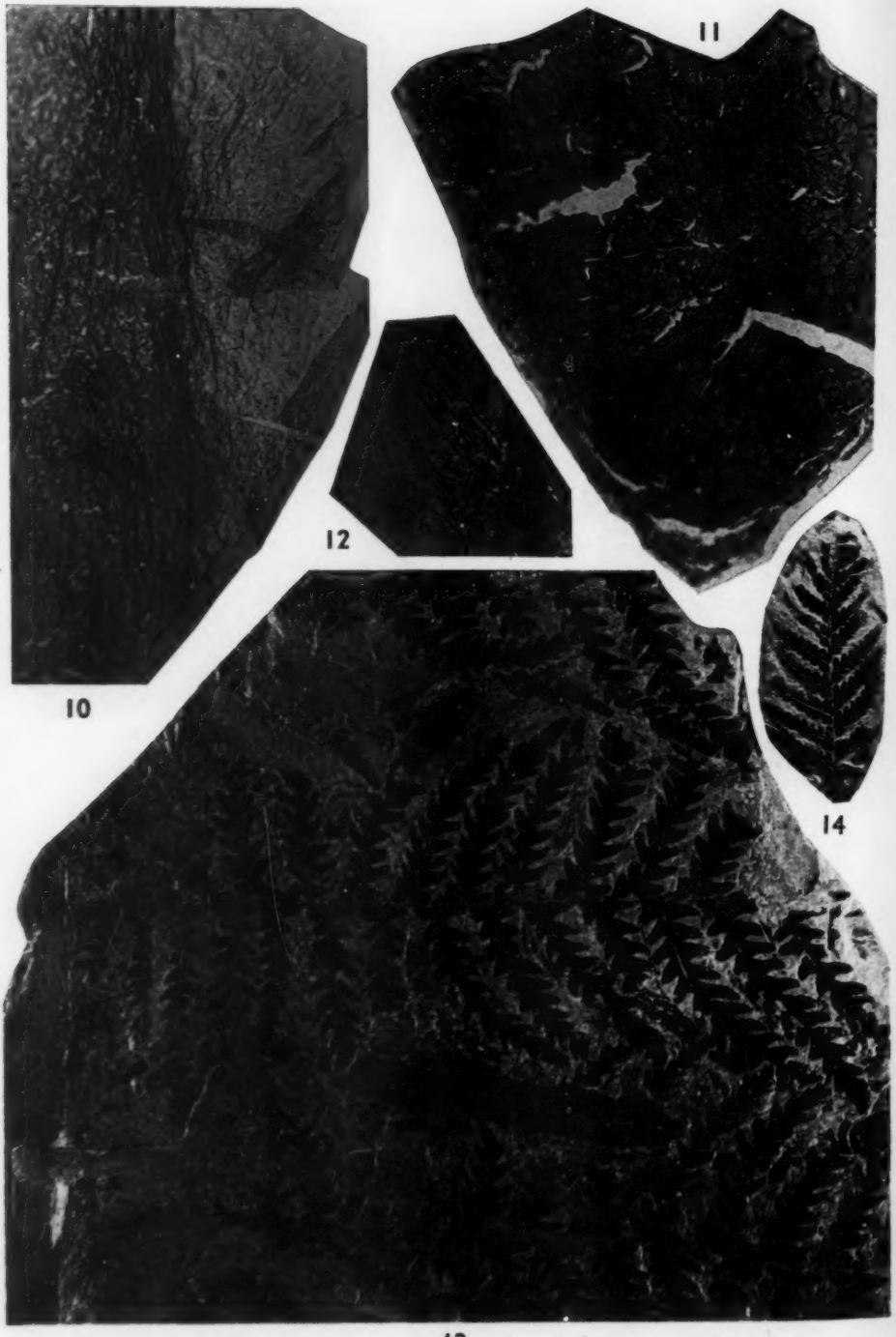
Figs. 4, 5. A single sporangium shown under different lighting conditions to bring out the cellular details of the wall; x 110 and x 80 respectively.

Fig. 6. A hair showing the characteristic septate structure; x 440.

Figs. 7, 8. Sporangial masses as they appear after partial oxidation of the sporangium wall; both x 150.

Fig. 9. A single mature spore; x 440.

ANDREWS—AMERICAN CARBONIFEROUS FLORAS. VI



ANDREWS—AMERICAN CARBONIFEROUS FLORAS, VI

Explanation of Plate

PLATE 11

Pecopteris plumosa var. *dentata* (Bgt.) White

Fig. 10. Cuticle; central heavier band represents the leaf margin, the dorsal (lower surface) cuticle is adjoined on the right. x 140.

Fig. 11. Ventral cuticle from the area between the branches of a bifurcated lateral vein; x 140.

Fig. 12. Dorsal cuticle at leaf margin; marginal zone at the right; x 140.

Fig. 13. Portion of a frond showing the primary rachis at the left and parts of three secondary pinnae; natural size.

Fig. 14. Pinnule of more delicate structure; x. 7.

Explanation of Plate

PLATE 12

Senftenbergia plumosa var. *Jonesi*

Fig. 15. Portion of pinna rachis showing the epidermal hairs; x 6.
Fig. 16. Apical portion of a sporangium; x 95.
Fig. 17. Branching epidermal hairs; x 440.

Scolecopteris Radforthii

Fig. 18. Portion of an ultimate pinna showing venation of the pinnules; x 10.
Fig. 19. Lower surface of a pinnule showing the compressed synangia; x 20.

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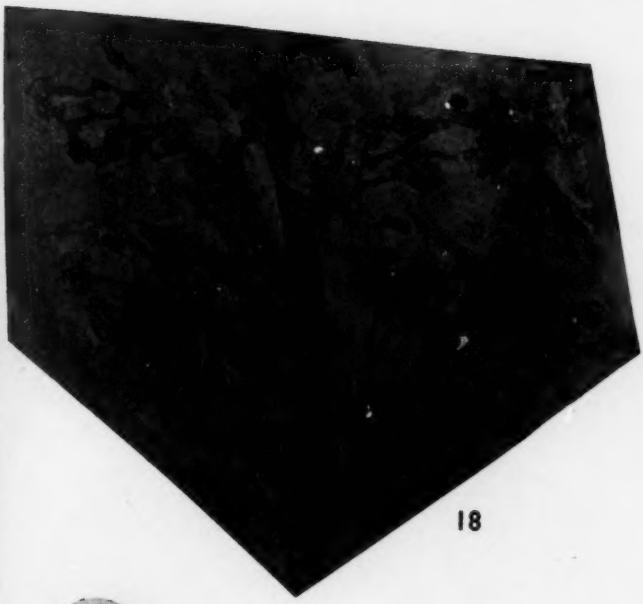

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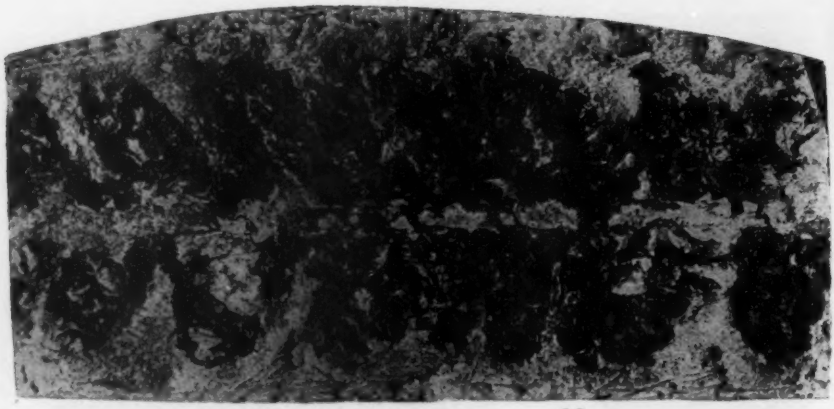

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ANDREWS—AMERICAN CARBONIFEROUS FLORAS. VI

Explanation of Plate

PLATE 13

Scolecopteris Radforthii

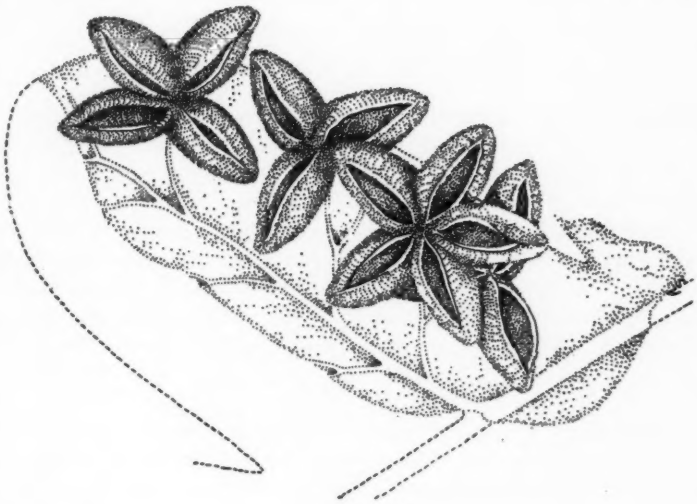
Fig. 20. Portion of an ultimate pinna; x 10.
Fig. 21. A partially macerated synangium showing two spore masses and part of a third; x 135.
Fig. 22. A single isolated spore mass; x 135.

Explanation of Plate

PLATE 14

Scolecopteris Radforthii

Figs. 23, 24. Showing the synangia before and after dehiscence.



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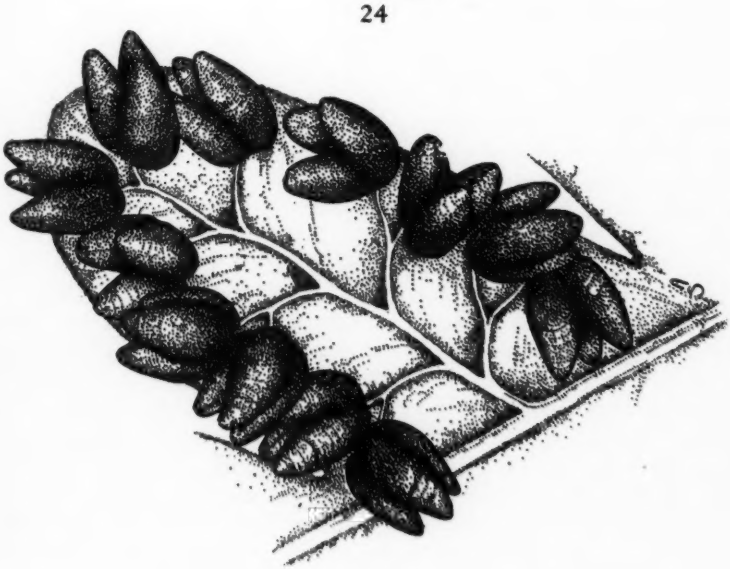

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ANDREWS—AMERICAN CARBONIFEROUS FLORAS. VI

SOME HOURLY OBSERVATIONS OF TREE GROWTH

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Although everyone has observed the active response of trees to the seasons, yet trees are often thought of as static organisms,—capable, it is true, of performing certain functions in certain seasons or even remaining quiescent during the cold of winter but without the capacity of immediate adjustment to slight changes in environment. The habit of producing leaves in spring is generally associated with the increasingly warmer and brighter sunshine of that period. Likewise, the unfolding of flowers, the development of fruit, and the autumnal coloration are dependent upon seasonal changes in weather. These reactions are annually observed and appreciated. It is not generally known, however, that the duration of sunshine for any one day may require a profound adjustment on the part of the tree.

Numerous investigations have been made on the effect of environmental conditions upon tree growth. The literature contains many references to the response of trees to one or more meteorological phenomena. However, all the factors which have an effect upon the growth rate have not been studied simultaneously, nor have continuous and automatic records of them been made.

This study was undertaken to determine, if possible, the effect of weather upon the physiological processes of a tree. Since most physiological activity is finally manifested as growth, it was believed that a continuous record of growth—known to be of seasonal occurrence—might be correlated with the prevalence of certain external factors exhibiting similar periodicity. Thus, the conditions peculiar to early spring (abundant moisture, low temperature, short days, etc.) might show a correlation with the beginning of growth, or with its gradual decline upon the approach of summer. After the growth peak had passed other conditions would prevail (those of late summer, for instance, with longer days, less moisture and higher temperatures); and again a continuous record might show certain physiological relationships which in turn would differ from those of winter. Thus if the entire range of temperatures, seasonal amounts of sunshine and of precipitation are checked against the carefully recorded responses of the tree, certain individual and combined influences of these environmental factors might be reflected in its growth. The work herein outlined is intended as a preliminary report. Since identical weather conditions are of infrequent occurrence, many of the recorded relationships of these factors to tree growth have not been repeated, and the following discussion is based largely upon extreme conditions.

A critical study of tree growth must take into consideration both the systems of photosynthesis and translocation peculiar to trees. While this study does not specifically touch upon either system, the interpretation of the accumulated data

might have a bearing upon these problems. Since Curtis[1] has exhaustively discussed the literature and indicated the present status of the work while Gibbs[2] has cited an additional several hundred papers, no further bibliographical references will be made in the discussion to follow.

For this study a Bur Oak (*Quercus macrocarpa* Michx.) 34 years old was selected. This tree grew near the center of a small group of mixed White and Black Oaks and had received little pruning. The growth rate had been normal and as it had never been suppressed the tree developed a low wide-branched crown with a trunk 30 inches in diameter, 1 meter above ground level. Every effort was made to permit the tree to grow independent of any artificial stimulus, and throughout the period of observation it received no pruning, spraying, fertilizing or irrigation. This report covers a period of 70 weeks, from July 16, 1933, to November 25, 1934.

METHODS

During this investigation the dendrograph record was used as a basis for evaluating the effects of all the environmental factors. All external conditions which appeared to exercise some influence upon the growth of a tree were charted. Thus a continuous and automatic record was made of the air temperature, relative humidity, hourly wind movement, barometric pressure, precipitation, sunshine and soil temperature. Simultaneously, identical graphs were made of the expansion and contraction of the trunk by the use of the dendrograph, while the internal temperature and internal pressure were recorded automatically.

Since most of the instruments must of necessity be placed close to the tree under observation, a rectangular concrete block weighing approximately .95 kg. was cast within .3 dm. of the trunk to serve as a table. A shed 3 m. long, 1.3 m. wide and the same in height was built to enclose both the lower portion of the tree trunk and the concrete table. This shed was fitted with two large ventilators, one in the roof and another in the west side. The east side opened into a door, and the side walls extended to within 2 dm. of the ground level. This type of construction provided safety and shelter for the instruments during inclement weather, and at the same time allowed ample ventilation for accurate records. The sun record was taken on a roof several hundred meters from the tree. The barometer was located in a building approximately the same distance away. The hourly wind movement and precipitation records are from the St. Louis Office of the Weather Bureau, located about 7 km. from the tree. All other instruments were placed in the house built about the tree.

DENDROGRAPH

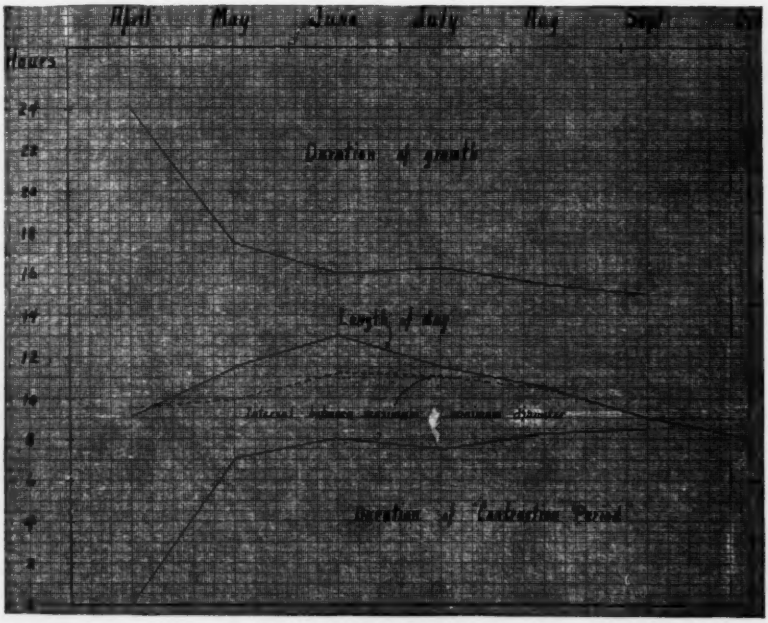
This instrument was developed by MacDougal[3], who has also carefully de-

[1] Curtis, O. F. The translocation of solutes in plants, New York, 1935.

[2] Gibbs, R. D. Studies in tree physiology I. Can. Jour. Res C 17:460-482. 1939; II. C 18:1-9. 1940; III. C 20:236-240. 1942.

[3] MacDougal, D. T., J. B. Overton, and G. M. Smith. The hydrostatic-pneumatic system of certain trees: movements of liquids and gases. Carnegie Inst. Washington Publ. 397. Washington, 1929.

scribed it and calculated its accuracy. It is capable of providing a continuous and accurate record of all tree-trunk fluctuations. Changes in diameter of a tree trunk being essentially manifestations of growth, the dendrograph becomes the most important instrument in a study of growth and the factors affecting it. For this study it was attached in the usual manner. The contact points touched a smoothed portion of the trunk, on opposite sides, about one meter above the ground. Since the contact rods touched the newer layers of the phloem the record is essentially a measurement of the actively growing portion of the tree. What influence external conditions have upon the xylem alone cannot be determined from this record.



Relation of daylight to tree growth.

In spring, about ten days after the initial swelling of the buds but before they reach 1½ inches in length, the dendrograph shows a marked daily rhythm in expansion and contraction. The peak of the expansion is reached between 4 A. M. and 6 A. M. At exactly 6 A. M.—on sunny normal days—the trunk begins to contract, reaching its smallest diameter for the 24-hour period at 4 P. M. From then no change occurs until exactly 6 P. M., when the expansion begins and continues until the following morning at 6 o'clock. This rhythm is constant on clear days when the tree is in leaf. However, during rain—no matter how slight

—and on cloudy or humid days the rhythm is temporarily interrupted. At such times the tree fails to contract in the period from 6 A. M. to 4 P. M. Should only a part of the forenoon be cloudy and the rest with full sun, contraction may begin later and last only a short time. Even the normal expansion, which begins at 6 P. M., may be delayed until midnight or after and it may continue until noon of the next day. This variation of the normal rhythm is only temporary, however, and the first cloudless day usually establishes the daily expansion and contraction. The degree of expansion and contraction and the length of the quiescent period, after attaining either the maxima or minima, are dependent entirely upon the sunshine and the relative humidity. Thus a cloudy day in midsummer shortens the contraction period as much as three hours; the minimum may be reached at 1 P. M. During that same morning the contraction period may have been delayed two hours; or until 10 A. M. Since the dendrograph record indicates that a certain amount of the daily expansion is dependent upon water absorption, the contraction must be the result of water loss. In this manner, the daily growth is obscured except as it shows in the slowly rising peaks of the dendrograph record.

All growth in diameter occurred between April 10 and June 7, a period of ten weeks. No growth is evident in the record after June 7, although this is the period during which the "summer wood" is usually expanded. The fact that during cloudy humid weather, in the absence of any notable contraction, there still exists a rhythmic increase in diameter, seems to indicate that whatever growth occurs is accomplished after midnight, the period during which this increase is normal. If the rhythmic diameter changes are accepted as indications of water loss or absorption, then the dendrograph clearly shows how minute is the lag between utilization and replenishment. The dendrograph reflects the condition of the cells adjacent to the point of contact on the trunk, in this case a halfway point between utilization of the water by the leaves and replenishment which is the function of the roots. Therefore, the rhythmic contraction beginning at 6 A. M., when only the top of the tree is exposed to the full morning sun, indicates that the effect of evaporation from that part is almost instantly felt throughout the tree. The rhythmic diameter changes occur throughout both the growing and the summer periods. Approximately two weeks previous to the shedding of the leaves the dendrograph record becomes a straight line and remains so except for minor fluctuations correlated with the internal temperature. At this time the cooling effect of actively transpiring leaves gradually diminishes, and the internal temperature gradually rises until the typical dormant record is produced. This is unmodified by transpiration and fluctuates as widely as the air temperature. Thus a close study of both the dendrograph and the internal temperature records will reveal the approximate hour during which the formation of the abscission layer begins. It will also show the time required for this formtion to affect all the leaves, thereby designating the hour of dormancy. The reversal of this process—the change back to rhythmic fluctuations—will, during the following spring, designate the hour of awakened physiological activity.

During extremely cold weather, when the internal temperature is finally lowered to —7° C., the tree immediately contracts and remains contracted until the temperature again rises. The contraction during times of extreme cold is in a straight-line relationship to the internal temperature. After the initial sharp contraction at —7° C., the diameter of a tree varies exactly as the internal temperature varies.

INTERNAL TEMPERATURE

To obtain this record a soil-thermograph was inserted in a 20-mm. hole bored through the trunk to within 80 mm. of the opposite side. Afterward a plug of asbestos was rammed in, leaving only the flexible tube extending. The entire opening was then sealed over with an asphaltic compound.

During the dormant period the record taken by this instrument is simply a smoothed curve of the air temperature, exhibiting whatever lag the insulating efficiency of the tree trunk imparts. Usually the internal temperature remains about 8° F. lower than the maximum summer air temperature, but it never exceeds 86° F. so long as the tree is supplied with some soil moisture. During the winter the internal temperature remains about 5° higher than the minimum. There are, however, rhythmic variations of internal temperature which are correlated with periods of stormy and fair weather, as well as distinctive seasonal trends. During the period of growth and its cocomitant transpiration the record is closely linked with that of the dendrograph, the internal temperature being highest at the peak of expansion and coolest when the contraction is greatest. Incidentally, the peak of expansion and also of internal temperature occurs during the early morning hours, coincident with the lowest air temperature and the lowest evaporativity of the air for the previous 24 hours. There is a marked tendency toward higher internal temperatures, sometimes an immediate increase, following a rain during the growing period. Should either the precipitation or the accompanying cloudy weather last for 24 hours, the internal temperature slowly declines to a point well below the daily minimum. The initial rise is traceable to the lessened transpiration during the actual rainy period. The decrease below the daily low record seemingly is the result of the accelerated transpiration, since following a rain more water is available. After the initial rise the periodicity of the rhythm is reversed, the internal temperature varying inversely with the dendrograph until the stormy period has passed. The cool morning hours find the tree coolest. This would not be true when the air temperature dropped considerably after rains, for then the lowered air temperature, no doubt, is chiefly responsible. However, if evaporativity is closely related to air temperature a rise in internal temperature should follow such cool periods, since there would be less water loss from transpiration. In any event the individual effects of these phenomena cannot be separated, and in all probability both become operable under certain conditions and may mask their interlocking effects.

SOIL TEMPERATURE

The recording element of a soil-thermograph was placed 22 inches below the surface under the branch tips. This position was chosen after explorations showed the presence of a large number of "feeding" roots in this area. The soil surface around the tree and extending beyond the branch spread was without vegetation. During the summer the portion above the thermograph element received sun for only 1½ hours during the mid-day.

The record of the soil temperature discloses no great daily range, and the annual record appears as a smoothed curve of the internal temperature. In the absence of marked daily or weekly fluctuations, the effects of soil temperature could not be traced on the dendrograph. Thus, although this factor does not have an hourly effect upon the tree it probably does influence the seasonal occurrence of growth. In this connection it is interesting to note that all spring growth in diameter occurred within the comparatively narrow limits of 15° F. Growth began in April coincident with a soil temperature of 50° F. and ceased the first week of June with a soil temperature of 65° F. A maximum of 78° F. was reached in July; the minimum, 29° F., during the first week of March. Comparative figures of soil temperatures from more exposed situations are not available, but it is certain that they were higher during the dry spring and very dry hot summer. Whether the heat reacted unfavorably upon the trees is not known. The temperature recorded under the tree observed was probably not inhibitory to growth; insufficient water seems more likely to have been the limiting factor in the period after June.

PRECIPITATION

This record, as well as the wind record, was taken from the St. Louis Office of the Weather Bureau, a distance of about 7 km. from the tree. During most of the year duration of rain at the two stations is practically the same, and the total precipitation does not usually vary greatly. However, during the hot dry months of June, July and August, weather conditions may be altogether different at the two stations. It is during these hot dry spells that the effect of precipitation is most easily determined, and for that season the record is simply an observation.

Certain periods of the dormant season are generally considered as devoted to water storage. However, the effects of rain were noted only during the summer, when even slight amounts (.01 inch) were recorded by an upward rise in the dendrograph. The abruptness of the rise and its continuance depended entirely upon the total rainfall. Precipitation of only .01 inch was beneficial chiefly because of the humid conditions prevailing at the time. Much more rain was necessary to percolate sufficiently to reach the roots. The reaction to larger amounts of rain, which in 1933 and 1934 occurred only in very early spring, are not easily discernible. In spring, the tree is usually well supplied with moisture, since transpiration has not reached the peak of midsummer and temperatures are uniformly lower. Therefore, slight fluctuations in both the dendrograph and the records of

internal temperature cannot be interpreted as resulting solely from rain. It is hoped that future less droughty years will yield a record showing the effect of substantial rains in midsummer. During the fall of both 1933 and 1934 there was an abrupt increase in tree diameter coincident with the beginning of the seasonal rains. That this increase was not maintained may have been due to the extremely dry weather characteristic of the winter following. Other more favorable seasons might show the late September increase coincident with the fall rains to be of a permanent character. The absence of any marked diameter increase after rainfall, in either fall, winter or early spring is difficult to account for, since both water loss and gain, as well as growth, are charted in the dendrograph record and can be easily separated.

RELATIVE HUMIDITY

A continuous humidity record was obtained from a hygro-thermograph placed on the concrete block in the shelter previously described.

Throughout both the "growing" and the "summer" seasons, during clear weather, the humidity is highest between midnight and 4 A. M. Then it begins to decline and reaches the lowest point about noon. Changes in relative humidity affect the evaporating power of the air and consequently alter the transpiration rate, as is clearly shown in the dendrograph record. Both the humidity record and the dendrograph record show a peak in the early morning hours. The humidity declines first, and shortly after the dendrograph records a contraction of the trunk. Since the relationship between tree diameter and humidity is so close any factor capable of modifying the humidity will affect the tree sufficiently to be incorporated in the dendrograph record. On cloudy days, which are usually accompanied by higher and more nearly uniform humidity, the tree undergoes only a limited contraction. The more uniform dendrograph record continues as long as the humidity remains above that of normal bright days. During the cooler portions of late summer, the dendrograph shows a delay in the beginning of the contraction period coincident with the presence of dew. While the almost instantaneous responses of the tree to changes in relative humidity have been demonstrated, the fact remains that the daily period of contraction begins at 6 A. M. regardless of the average monthly humidity readings, which tend to decrease from April to July and to increase toward October. Thus the average monthly humidity readings for 1943 show:

	7 A. M.	7 P. M.
April	64%	57%
May	59%	43%
June	66%	49%
July	61%	42%
August	73%	59%
September	86%	72%
October	74%	54%

Since humidities do not tend to be lower in midsummer than during other growing seasons, seasonal shifting of contraction and expansion periods following

the daylight hours is not reflected in the humidity reading. Essentially, humidity changes affect the tree instantaneously and therefore show no seasonal rhythm.

WIND MOVEMENT AND AIR TEMPERATURE

These two factors show no seasonal trend. The wind movement remains nearly constant throughout most of the growing season. Its effect upon the tree is immediate, and we have observed a very rapid rise or fall in internal temperature due to accelerated wind movement prior to a thunderstorm. The air temperature gradually rises to a peak in summer and then declines. Apparently it has only a limited effect upon the tree, since any rise or fall in air temperature is usually correlated with certain very definite weather changes, and it would be reflected in other records.

BAROMETRIC AND INTERNAL PRESSURE

Certain of the hourly charts indicate an interesting relationship between barometric pressure and the behavior of the tree. However, the precise effect of a rising or falling barometer must be left to a subsequent study more concerned with a shorter time interval than used in this study. The internal pressure, an extraordinarily interesting measurement of the activity of a tree, has been reported upon.[4] These two factors are again without seasonal trend, and since their effect upon the tree is instantaneous, the records obtained must be read to a very short time interval, perhaps 5 minutes or less.

SUNSHINE

The length of day, changing as it does from season to season, might be expected to exert a profound influence on the behavior of a tree. That it does is apparent from the dendrograph record and also from the internal temperature. In April the interval in the daylight hours between maximum and minimum diameter is only 9 hours, in May it is 9.9 hours, and in June, with 13 hours of sunshine, it increased to 11.3 hours. This means that as the sun rises earlier toward the latter part of June the tree begins to shrink early in the morning and reaches and maintains its small diameter later in the day. During this early period, when active growth is taking place, the effect of sunshine is very marked, although the contraction or expansion of the trunk is not as closely tied to length of day as it is through the months of August and September. During the late fall contraction begins with sunrise, and expansion begins with sunset. It is known, however, that in addition to seasonal trends sunshine does cause an immediate change in the activity of a tree. Some evidence exists to show that the passing of each cloud on an otherwise clear day modifies the functions of the tree to the extent that they can be recorded. Thus the dendrograph and the internal temperature readings both leave a record indicating the passing of a cloud. The immediate effect of

[4] Beilmann, August P. An attempt to record internal tree-trunk pressures. Ann. Mo. Bot. Gard. 27:365-370.

sunshine on a tree will be the subject of later investigation. As a general thing, a bright sunny day accelerates transpiration, depresses the internal temperature, and initiates the beginning of the contraction period.

SUMMARY

Several thousand weekly charts have been obtained from a series of automatic recording instruments. These show some interrelationship between "weather" at a particular hour and some modifications to it on the part of the tree, depending upon whether or not the external factor favored or inhibited growth.

The dendrograph has proven of value in recording seasonal trends but some modification of the instrument is required for a critical study of tree behavior.

The internal temperature shows a seasonal trend but is equally important for a short-time study. It is rather difficult, however, to localize the reading and in this study the average of the trunk diameter was obtained.

The soil temperature is a seasonal factor playing a role at the beginning and perhaps at the end of the growing season.

Precipitation, as might be expected, is seasonal and exhibits a pronounced effect very quickly when it occurs out of season. A calculation from October to October probably gives a clearer picture of the moisture need and utilization of the tree than does a record based on the calendar year. During a very dry portion of the year the tree immediately reacts to any form of moisture whether rain, dew, or high humidity.

The hourly wind movement and the maximum wind velocity are without seasonal effects. Wind cannot be dismissed, however, since observation has shown a striking relationship between velocity and internal temperature.

The air temperature varies with the season, and does not show either marked seasonal trends or rapid effects, largely because all other factors are changing just as rapidly. For instance, since a very sharp rising or falling temperature may be accompanied by rain, on the one hand, and a dry period, on the other, the effects are lost in the other records.

The barometric pressure and the internal pressure might be expected to yield some interesting records. However, the effects seem to be lost in any seasonal study of behavior. They may be investigated in a study dealing with a short-time interval.

SEGREGATION, MUTATION, AND COPULATION IN SACCHAROMYCES CEREVISIAE[1]

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HAPLOPHASE CULTURES

Some individual ascospores from 4-spored asci of *Saccharomyces cerevisiae* germinate to produce haploid cells which persist in the haplophase, thus producing entire cultures containing only haploid cells. We ('43c) have reported a new method of hybridizing yeasts by mixing haplophase cells of different origin in broth. The mixtures result in copulations between different haplophase cells if each culture is paired with its complementary type. The diploid hybrid cells produced by copulation are capable of forming asci containing 4 viable spores.

Šatava ('18) and Winge and Laustsen ('37) showed that some of the single ascospore cultures from many recognized species of *Saccharomyces* contain only round, or roundish, rather small, haploid cells. They observed these cells fuse in some cultures to produce dumbbell-shaped zygotes from which elongate vigorous diploid cells arose by budding. These investigators all agree that such haploid cultures are obviously the equivalent of *Torulae*[2], and Winge and Laustsen attempted pairings of the standard species of *Torula* which were available in Copenhagen. They remarked, "In no instance did the pairing inoculations give rise to ascus formation. But this negative result was really to be expected as all Saccharomycetes appear to be asexual or homothallic." Their conclusions may be influenced by the fact that they observed copulations between haploid cells and ascospores in preparations held between slide and cover-glass so tightly that the cells spread out in two dimensions only. This gave beautiful photographs but may not have permitted sufficient freedom of contact to make preferences in copulation obvious. Our conclusions were based on genetical analyses rather than microscopic observations and were confirmed by controlled matings of haplophase cultures. They made no attempts to pair the haplophase cultures which they obtained from *Saccharomyces*. Šatava observed that ability to sporulate is restored by fusion of haplophase cells but apparently he made no direct efforts to pair haplophase cells from different cultures.

Winge and Laustsen considered the haplophase to arise by standard reduction and segregation of a diploid nucleus in the conventional manner (which seems to

[1] This work was supported by a grant from Anheuser-Busch, Inc., Saint Louis.

[2] From a strictly taxonomic point of view, the name "*Torulopsis*" should be used, for *Torula* had already been applied to another genus when it was first suggested by Hansen. However, since Hansen and all other investigators of industrial yeast have used "*Torula*", we are following their example in this article.

us the most acceptable view), while Šatava is rather vague about the relationship of haplophase and diplophase. Šatava found these "reduced" (haplophase) forms much different from standard diploid yeasts in their ability to produce spores and "die Zellen von normalen Form zu bilden." He attempted a classification of the degree of deviation of the haplophase from normal which agrees generally with our own observations. Winge and Laustsen were much more precise, and probably more accurate, in distinguishing between haplophase and diplophase. They observed the diplophase to originate either (1) by direct germination from a single, originally haploid, ascospore (text-fig. 2) or (2) by the delayed fusion of two haploid cells arising from the same haploid ascospore. In the former case, the nucleus in the originally mononucleate spore divided to produce two nuclei which fused in the new bud. They found cultures originating by direct diploidization to be degenerate in many ways, and this fact has been confirmed in our experience. We have observed that when a haploid ascospore germinates directly as a diploid cell to produce a small colony, it often dies before transfer can be made. On the other hand, when a single-spored ascus from a diploid colony germinates, it usually grows out directly as a diploid cell and is apparently fully vigorous and identical with the original form. In this case it seems probable that the original spore was diploid rather than haploid.

The first two types of diplophase cultures arising from haploid single ascospores are homozygous. Winge and Laustsen observed that homozygous diplophase cultures vary extremely in their ability to produce spores, and that the spores produced are generally of diminished viability, facts which we have confirmed. They stated that the haplophase never produces spores, but to this we have found some rare exceptions. However, the spores produced by the haplophase are much inferior in vigor to those arising from the diplophase. For example, one of the variants of the round-celled haploid culture *A*, described below, produced spores in round asci the same size as the vegetative cells, thus proving that the spores had arisen parthenogenetically. Four intact 3-spored asci and eight single ascospores from two 4-spored asci were isolated on nutrient medium and failed to produce viable cultures.

The simplest criterion for distinguishing haplophase from diplophase is difference in cell shape and size. This is not a perfect method although the large ellipsoidal true diploids are easily distinguished from the small spherical true haploids. However, some haploid cells are regularly elliptical but smaller than the corresponding diploid and there are many intermediate types. Inspection of many cultures has confirmed the view that many single ascospore cultures are haploid and remain haploid. Haploid cultures are much more variable than diploid cultures. Several rough variants practically always appear when a suspension of haploid cells is plated on an agar surface. Winge and Laustsen remarked on the fact that haploid colonies contain many sectors; that they are generally smaller than diploid colonies has been observed by Winge and Laustsen, and Šatava, an observation which we have confirmed. Variation in shape of cells also occurs, and

haploid colonies originating from small spherical cells often contain large numbers of balloon cells and long slender fibrous cells. Old broth cultures contain cells described as "ameboid" by Šatava. He doubtless had these characteristics in mind when he stated that the extreme reduced forms were unable to control cell shape. According to our interpretation these so-called ameboid forms in old broth cultures are copulating cells. The variability of colonial forms in haploid cultures is due to the fact that recessive mutations occurring in the haplophase are immediately revealed in the phenotype. A diploid culture may be equally mutable but the "opposite number" normal allele is dominant and the mutation does not come into expression. The mutated genes present in a normal, smooth-colonied, wild-type, diploid cell are revealed when four spores are dissected and each is grown separately. Almost invariably none resembles the parent culture.

THE "ROUGH" CHARACTER

The most useful diagnostic character differentiating various haplophase cultures is the so-called "roughness" of the colony grown on solid medium. The tendency to classify yeasts as "rough" or "smooth" is not a fruitful approach to the subject. Smoothness is the wild-type character which distinguishes the form capable of successful competition under natural conditions. It depends on the fact that the cells do not cohere to form a specific pattern, but daughter cells separate quickly from mother cells and each new unit falls smoothly into place making the colony a round hemispherical structure on the solid substrate. Roughness depends on the cells clustering in such a way that a definite pattern results when the macroscopic colony reaches its full growth. The basic pattern of aggregation is observable in microscopic examination of the cells from broth cultures, for rough types generally bud in various "rosette" forms.

Winge ('35) has described the "figure 8" arrangement of haploid cells prior to copulation (text-fig. 2). After a bud has reached full size, two new buds appear (one from the mother and one from the daughter cell) near the point of union of daughter and mother cell, producing a "4-leaf clover" effect. Most "rosettes" originate in a variation of the "figure 8" formation. Many of these cultures make what appears to be homogeneous suspensions because the "rosettes" are too small to affect the turbid appearance produced when the culture is suspended in fluid medium or grown on broth, but the extremely rough colonies cannot be easily brought into a homogeneous suspension and when rough-type yeasts are grown in liquid medium the supernatant liquid is completely clear. This is a character much desired for wine yeasts, especially for champagne yeasts. There is a basic pattern of cohesion even in extremely smooth cultures, for nearly all colonies show some distinctive topographical structure if grown on solid medium long enough to form a giant colony. Conversely, when moderately rough colonies are sown heavily enough on agar to prevent the formation of large colonies, only smooth ones appear. On an unevenly spread plate one finds an outer fringe of extremely rough, large colonies surrounding a central group of small,

smooth ones. All belong to the same genotype but the rough character cannot come into expression until the colony attains considerable size.

We have observed several hundred different types of rough-colonied yeasts, and although each one is distinctive and recognizable and can be duplicated and recognized when transplanted, we have not thus far discovered any exact duplicates. The range of variation is extremely great. In addition to the fundamental "rosette" or budding pattern, differences in shapes and sizes of the cells affect the colonial form. In all colonies the variation in cell size increases with age, generally in the direction of producing larger cells. As a rule, rough colonies contain more elongate cells than smooth colonies, and part of the basis for extreme roughness is possibly the maintenance of end-to-end connections after cell division which has been described so frequently in the genus *Bacillus*.

All four cultures from the single ascospores isolated from a 4-spored ascus originating from stable, smooth-colonied, wild-type diploid cultures of *Saccharomyces cerevisiae* are usually rough-colonied. This proves that the genes differentiating rough from smooth colonies are recessive and several loci are involved. The wild-type "opposite number" alleles of the mutant genes prevent them from coming into expression in the heterozygous wild-type diplophase. Although we have dissected many asci from the same diploid culture, practically no duplicate cultures have been found among the colonies grown from the single ascospores, which indicates that the diploid cell is heterozygous for a considerable number of mutant genes and that many loci affect the characters lumped into the so-called "rough" class.

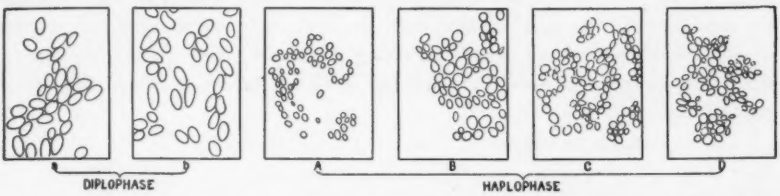
SEGREGATION AND MUTATION OF HAPLOID CULTURES

Plate 15 shows photographs of four single ascospore cultures isolated from a single ascus of the M strain. They are all in the haplophase. Usually some of the single ascospore cultures from one ascus are diploid, but we have not found any regularity in the distribution of haplophase-diplophase types indicating that the character is the result of interaction of several genes. The data presented here are merely part of an extended pedigree of the M strain, but since no new points beyond those already recorded in earlier papers were established the entire pedigree is not reported. The ascus mentioned above was derived from an inbred culture. In the inbreeding process an intact 4-spored ascus selected from the original M strain was isolated and formed a colony. This colony was plated on agar and a single colony from this plate was selected and induced to sporulate. An intact 4-spored ascus was again selected from the best sporulater, grown alone, induced to sporulate, and an ascus from this second generation was the origin of the third-generation colonies shown in pl. 15.

Plate 16, figs. a and b, show the diplophase cultures obtained from the colonies grown from two intact 4-spored asci. A study of cell shape and size of the six cultures showed that the single ascospore cultures were haploid while the two cultures obtained from intact asci were diploid. Drawings of the cells on the same

scale are shown in text-fig. 1. The diploid cells are long and ellipsoidal in contrast to the round cells from the haploid cultures.

The colonies of the diploid cultures are uniform provided they are plated on agar before spores form spontaneously. If they are left a few weeks on an agar plate and then plated again on agar, variations appear due to the germination of ascospores which have formed in the colony. The large colony size is evidence of the vigor of the diplophase.

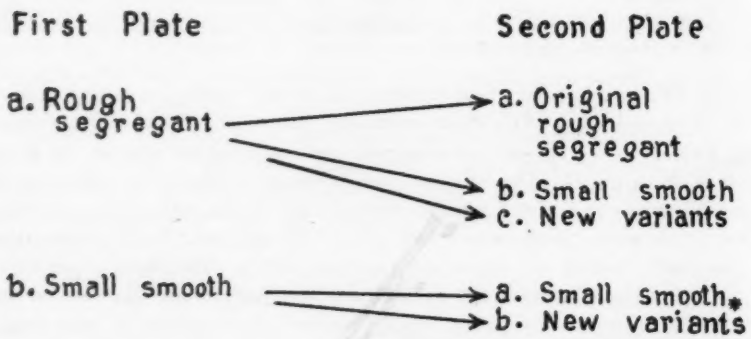


Text-fig. 1. Outline drawings (copied from photographs) of the cells from the six cultures shown in pls. 15 and 16.

The difference in colony type produced by the four haplophase cultures shown in pl. 15 are indications of the degree of heterozygosis of the diplophase from which they were derived. The original ascospores and the resultant colonies are designated *A, B, C,* and *D.* The different colony types are produced by segregation of genes at spore formation and multiplication of haploid cells, followed by mutation. These are the same cultures which were mated with each other in all combinations as previously reported (Lindegren and Lindegren, '43c). The earlier paper shows a photomicrograph of cell suspensions of the four cultures and reveals that the cells of the rough colony *(D)* produce "rosettes" characteristic of most rough colony types. Matings revealed that *A* and *D* belong to class a, while *B* and *C* belong to class α. Culture *A* is weakest and at the first plating produced only small colonies all of which were apparently uniform. However, in small colonies the phenotype is difficult to determine, since diagnostic characters are clearly shown only by relatively large colonies. On serial plating a large variety of colonies appeared. It does not seem profitable to report on these successive mutations since the data are simply a repetition of what has so frequently been described in bacteria. One fact was of interest, namely, that as selection and plating of colonies were continued, stable forms began to appear. These forms were all round-celled like their progenitors and therefore haploid. The weak culture *(A)* was more variable than the other three, and this is in line with observations on other strains, which indicate that a weak culture, once it is brought to a point of reasonably good growth, produces many more variations than stronger types—simply because the new mutations meet with less selection pressure from the mother colony type than in relatively more vigorous forms. As the *A* culture became better adjusted, by continued subculture, to the substrate on which it was plated, the variations became more obvious.

Cultures *B*, *C* and *D* show a characteristic feature of the more vigorous haplophase strains. The first plating generally shows a large rough colony accompanied by a smaller smooth form. (The cavities in the colonies reveal the places from which transfers have been made.) Transfer of the large rough colony produces the original rough type again accompanied by the small smooth form, with an occasional further departure in the shape of a new rough variant. This proves that the original rough type is the primary segregant while the small smooth form is a secondary mutation of the original segregant. This is further indicated by the fact that the small smooth form is much more stable than the original rough. Subculture of the smooth produces the smooth form almost exclusively, with only a few other variants which are often not generally comparable to the original segregant.

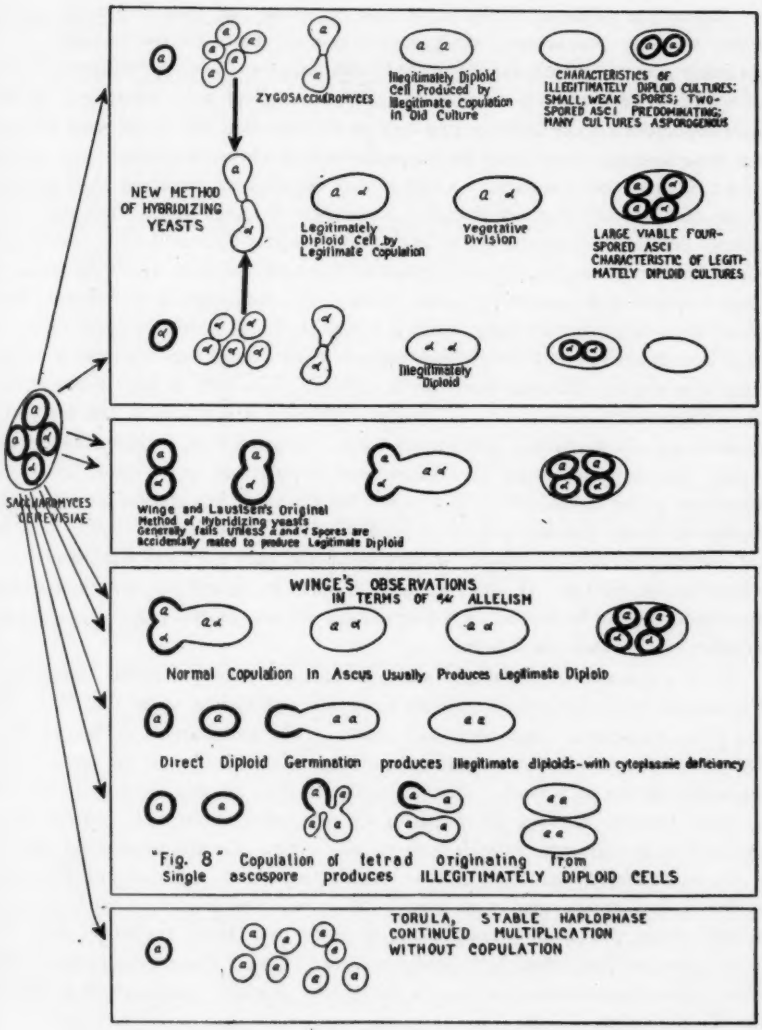
The sequence is as follows:



*These new forms are not generally comparable.

The four segregants shown in pl. 15 are characteristically different in colony shape and topography. The *D* culture is the roughest. The *C* culture produces the largest colonies and subsequent testing on a variety of sugars indicated that it was the best gas producer and the best yielder. The *A* culture, even after long subculturing, was much weaker.

Plate 17 shows the colonies of the four primary types obtained by subculture six months after the original isolation. The three photographs labelled "*A*" all show mutations of the *A* culture. Two of these are relatively stable while considerable variation is encountered in the third. The large colony size shows that some of these new variants have become fairly well adapted to the medium. The primary segregants from ascospores *B*, *C* and *D* are still rather clearly recognizable in spite of several serial transfers. They are generally much more stable than the *A* culture although many recognizable variants were obtained from each of them. However, so much variation occurred in the serial transfers of *A* that neither the original segregant nor the lines of descent can be traced.


ZYGOSACCHAROMYCES
Illegitimately Diploid Cell Produced by Illegitimate Copulation in Old Culture
CHARACTERISTICS OF ILLEGITIMATELY DIPLOID CULTURES: SMALL, WEAK SPORES; TWO-SPORED ASCI PREDOMINATING; MANY CULTURES ASPOROGENOUS
NEW METHOD OF HYBRIDIZING YEASTS
Legitimately Diploid Cell by Legitimate Copulation
Vegetative Division
LARGE VIABLE FOUR-SPORED ASCI CHARACTERISTIC OF LEGITIMATELY DIPLOID CULTURES
Illegitimately Diploid
SACCHAROMYCES CEREVISIAE
Winge and Lausisen's Original Method of Hybridizing yeasts Generally fails unless a and α Spores are accidentally mated to produce Legitimate Diploid
WINGE'S OBSERVATIONS IN TERMS OF αα' ALLELISM
Normal Copulation in Ascus Usually Produces Legitimate Diploid
Direct Diploid Germination produces Illegitimate diploids-with cytoplasmic deficiency
"Fig. 8" Copulation of tetrad Originating from Single ascospore produces ILLEGITIMATELY DIPLOID CELLS
TORULA, STABLE HAPLOPHASE CONTINUED MULTIPLICATION WITHOUT COPULATION

Text-fig. 2

Life cycle of *Saccharomyces cerevisiae*, showing relationship with *Torula* and *Zygosaccharomyces*.

COPULATIONS BETWEEN HAPLOPHASE CULTURES OF SACCHAROMYCES CEREVISIAE

Haplophase cultures of *Saccharomyces cerevisiae* fall into two main groups which we have provisionally designated a and α. Each culture is made up of potential gametes which can be mated with other cells of appropriate genetic composition from another culture. As the pure haplophase cultures age, illegitimate copulations occur between two cells of the same reaction in the same culture, but these matings rarely result in the production of characteristically large diploid cells. Diploid cells produced by illegitimate copulations are easily distinguished by smaller size and diminished ability to produce 4-spored asci containing viable spores. Matings between a and α haplophase cultures derived from a variety of strains of *Saccharomyces cerevisiae* produce large diploid cells which sporulate to form 4-spored asci containing viable spores. The procedure is as follows: One cc. of malt-dextrose dried yeast broth is placed in a 6 x ¾-inch culture tube. A large loop of cells from a broth stock culture is introduced together with a second large loop from a different broth stock culture. The tube is kept overnight in the refrigerator at about 10° C. The next morning it is placed in the incubator at about 26° C. where it is held for 48 hours. Inspection at 24 hours incubation usually does not reveal any copulations; new copulations appear after 24 hours, sometimes rather abundantly. The reason for the small inoculation is that in old haplophase broth cultures one often finds abundant copulations. These cells do not generally survive on transfer to new broth but only the small haplophase cells propagate the culture. If large amounts of cells are mixed the old homozygous copulations might be misleading. Copulations do not generally occur in colonies on agar; broth seems much better.

Only a fraction of the single ascospore cultures produces stable haplophases. We isolated stable haplophase cultures from other strains of yeast (*L*, *FLD*, 800 and 812) and paired these with each other in all combinations. The resulting diplophase was transferred to gypsum and the culture inspected for spores with the results shown in table 1. This test indicates that the a/α allelism is modified by other factors. Culture 28 copulates with all other forms and produces what appeared to be viable spores with both a and α types. On the other hand, several of the stable haplophase cultures were unable to copulate with any of the other strains against which they were tested. This was especially true with cultures isolated from the *FLD* strain whose pedigree has been published elsewhere (Lindegren and Lindegren, "*D*" family pedigree, '43b). These facts indicate that other factors superimposed on the a/α alleles may produce an excessively fertile or a sterile phenotype.

COMPARISON OF THE MECHANISM ASSURING CROSS-FERTILIZATION IN YEASTS WITH THAT IN OTHER ORGANISMS

Cross-fertilization in yeasts is necessary to assure the production of viable ascospores. A principal allelic pair of genes determines the copulating type to

TABLE I

RESULTS OF PAIRING HAPLOPHASE CULTURES FROM VARIOUS SOURCES IN ALL POSSIBLE COMBINATIONS.

	M 2	L 17	812 25	M 4	L 16	L 38	800 28
M 2		—	—	+S	+S	+	+S
L 17			+N	+N	+S	+S	+S
812 25				+S	+N	+	+S
M 4					—	—	+
L 16						—	+N
L 38							+S
800 28							

which a haplophase culture belongs. The situation in yeasts appears to be different from that in other living organisms, and the present discussion points out the characteristics of the various mechanisms for insuring cross-fertilization.

1. *Self-sterility alleles.*—Most hermaphroditic flowering plants are self-sterile due to a genetic mechanism which prevents pollen shed by the flower from growing down the styles of the parent plant. A mechanism that is probably fundamentally similar prevents the sperms of an individual hermaphroditic sea squirt, *Ciona,* from fertilizing eggs produced by the ovaries of the same individual.

2. *Sexual Dimorphism.*—In higher animals and some plants sexual dimorphism insures cross-fertilization. The genetic mechanism simply operates to reduce the probability of intersexes or hermaphrodites occurring.

3. *Plus-Minus Factors.*—This mechanism in *Rhizopus* is not a sexual mechanism because no unmistakeable sex organs are involved and therefore it cannot be called a self-sterility mechanism. It is more precise to consider it a special case in which a single pair of alleles controls copulation.

4. *Neurospora.*—We formerly called the alleles in *Neurospora* plus-minus factors, but later work has shown that they resemble self-sterility alleles more

closely than the factors found in *Rhizopus*. Both plus and minus thalli contain both male and female sex organs and self-fertilization is prevented. However, since the plus and minus thalli are both haploid and the zygote is invariably heterozygous for the same pair of plus-minus alleles this mechanism differs considerably from the standard self-sterility mechanism found in flowering plants in which a large series of multiple alleles exists and a great variety of heterozygotes abound.

5. *Hymenomycetes.*—The hymenomycete mechanism resembles the plus-minus *Rhizopus* mechanism rather closely since no obvious sex organs exist in these forms. It differs in the facts that in many hymenomycetes two loci are involved and that a multiple series of alleles at these loci further complicates the picture.

6. *Mating types.*—The mechanism which assures cross-fertilization in the single-celled diploid *Paramecium* resembles the plus-minus mechanism found in fungi since no sex organs are present, but the heredity seems to be more complex. The fact that the copulating cells are diploid is a still further difference from the most closely comparable fungal mechanism.

7. *Yeast.*—The mechanism in yeast is clearly different from the preceding. Our experiments indicate that monohybrid allelism modified by other factors controls copulation and we have given the symbol a/α to the principal allelic pair. However, the zygote is so much more vigorous than either parent that the diploid state produced by copulation has the character of hybrid vigor. In addition to insuring cross-copulation, heterozygosis for these factors results in a great increase in vigor, especially with regard to cell size and spore viability. The diminished vigor of the haplophase assures eventual supremacy of the hybrid in competition. Yeasts are quite different from most fungi since they propagate both as haploid and diploid cells and, in nature, balance, selection, and competition occur between these states. When the spores germinate in the spring the first growth may be haploid with one haplophase type competing with another until either legitimate or illegitimate copulation occurs, producing an even more complex state of competition. In the late fall sporulation occurs. Only the legitimate diploids produce viable spores and the cycle begins in the following year after these spores have germinated.

SACCHAROMYCES, TORULA, AND ZYGOSACCHAROMYCES

The diagram (text-fig. 2), showing the life cycle of *Saccharomyces cerevisiae* and including *Torula* and *Zygosaccharomyces* as phases of the cycle, has developed from the study of single-ascospore cultures. Stable haplophase cultures derived from *S. cerevisiae* fall into three classes: (1) those which do not copulate with any other strain, (2) those which copulate with all other copulating strains, and (3) those which copulate with their allelic partners only. The first type is a round-celled *Torula*, and Šatava ('34) pointed out that this genus is invalid because all *Torulae* have probably arisen from *Saccharomyces*. Illegitimate copulations occur in most old broth cultures of classes 2 and 3. Although the capacity of these illegitimate

homozygotes to produce spores is quite variable some of the cultures sporulate rather abundantly. They would be classified as *Zygosaccharomyces*. The spores in *Zygosaccharomyces* are probably inviable, but there are few, if any, records on the viability of spores in this genus. *Zygosaccharomyces* colonies are nearly always the rough type (Lochhead and Farrell, '31), another indication supporting the view that this genus contains single ascospore cultures of *Saccharomyces*. Conditions of copulation and sporulation seem in general to parallel each other, and illegitimate homozygotes which sporulated immediately on copulation would give the classical *Zygosaccharomyces* picture.

Dvornik ('38) recently studied spore formation in 50 strains of *Saccharomyces apiculatus*. They all formed one-spored asci. The vegetative cells bud characteristically with what appear to be abortive copulation tubes and resemble very closely some of the haplophase single ascospore cultures which we regularly obtain from *Saccharomyces cerevisiae*. The genus *Nadsonia* produces a peculiar type of polar budding similar to the "rosettes" or "figure 8" conformations found in single ascospore cultures. This genus may also be a peculiar type of single ascospore culture. These considerations indicate the inadvisability of giving generic or specific rank to peculiar types of yeasts incapable of producing asci containing four viable spores.

SUMMARY

Haplophase ascospore cultures derived from 4-spored asci of *Saccharomyces cerevisiae*, when paired with their complementary types, copulate to reproduce the original form.

Haplophase cultures originating from single ascospores of *Saccharomyces* resemble *Torulae* or *Zygosaccharomyces*. They are generally "rougher" and weaker than the diploid parent. The basis for the different rough characters is the inheritance of different types of budding and cell association. Variation of the haplophase is much greater than of the diplophase and the original segregant can be differentiated from the secondary mutants by serial plating.

The factors differentiating the copulating types seem to differ fundamentally from factors insuring cross-fertilization in other forms and were designated the a/α alleles.

Torula ("Torulopsis") and *Zygosaccharomyces* are probably invalid genera and merely represent phases in the life cycle of *Saccharomyces*.

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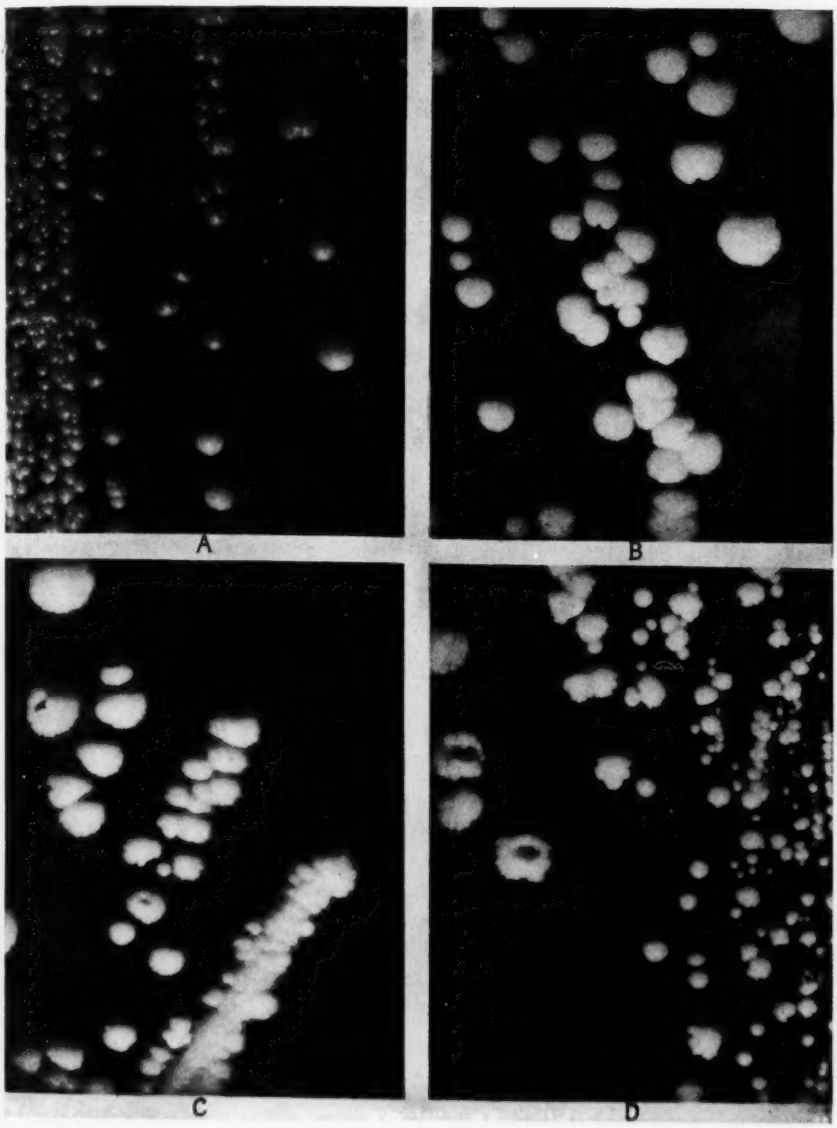
Explanation of Plate

PLATE 15

Saccharomyces cerevisiae

Colonies grown from the four ascospores dissected from a single ascus of the M strain.



LINDEGREN & LINDEGREN—SACCHAROMYCES CEREVISIAE

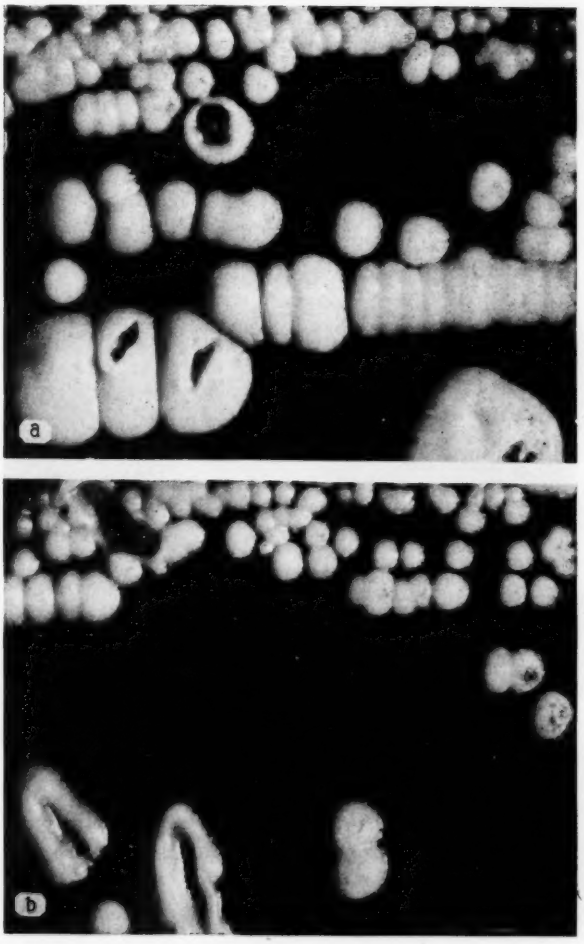
Explanation of Plate

PLATE 16

Saccharomyces cerevisiae

Fig. a. Diploid colonies produced by the self-fertilization of an intact 4-spored ascus from the same culture tube as the ascus from which spores *A*, *B*, *C*, and *D* of pl. 15 were obtained. When an intact 4-spored ascus is isolated and permitted to germinate, copulations usually occur before growth has progressed very far and the diploid cells soon outgrow the haploid ones. Diploid colonies are uniform and smooth in contrast to the haplophase colonies, which are generally rough and variable. These diploid cultures produce viable 4-spored asci while the cultures shown in pl. 15 do not.

Fig. b. A second culture obtained by self-fertilization of a 4-spored ascus in the same manner. Some cultures produced in this way are rough and cannot produce 4-spored asci. This is presumably because only a single spore in the ascus was viable.



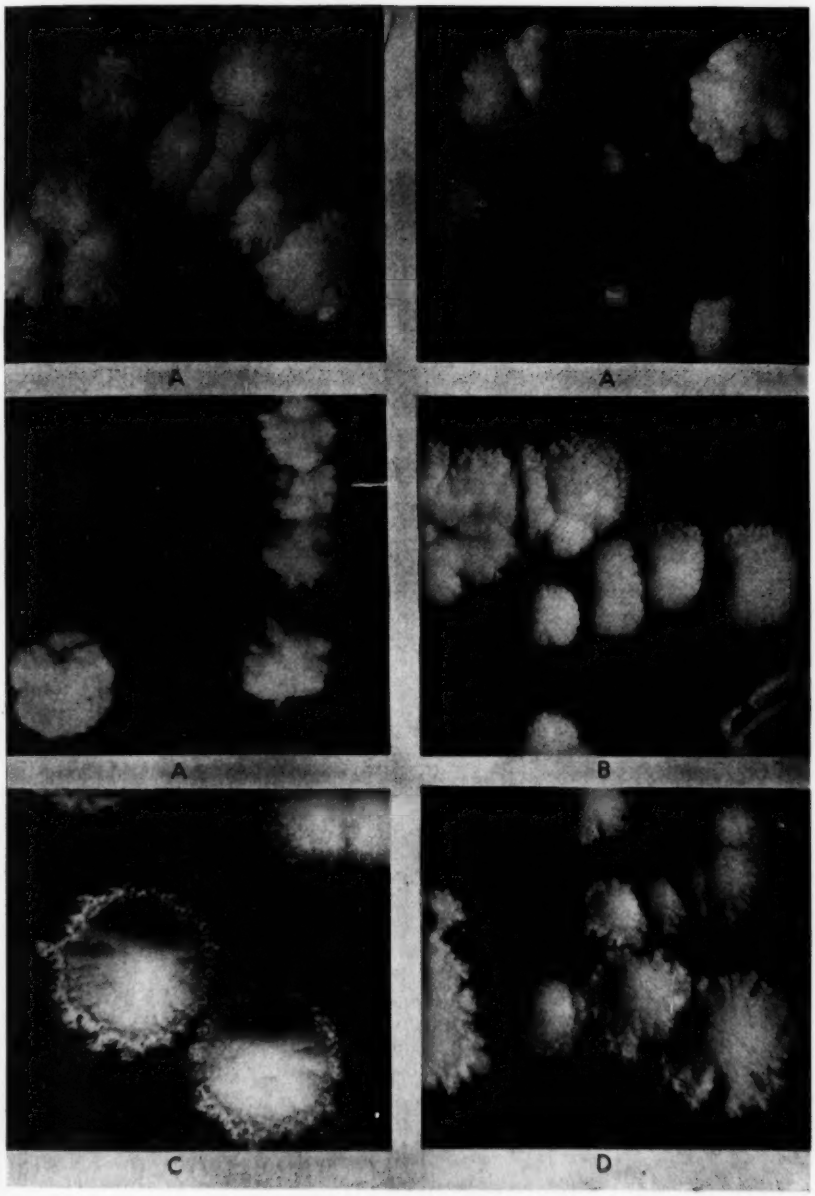
LINDEGREN & LINDEGREN—SACCHAROMYCES CEREVISIAE

Explanation of Plate

PLATE 17

Saccharomyces cerevisiae

Haplophase subcultures of the cultures shown in pl. 15 are reisolated six months after the original cultures had been grown from ascospores.



LINDEGREN & LINDEGREN—SACCHAROMYCES CEREVISIAE

A VARIETY OF MAIZE FROM THE RIO LOA

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In our collections of maize, two ears procured by Carl and Jonathan Sauer at a remote oasis on the Rio Loa in northern Chile are of particular interest. They are in various ways more like prehistoric Peruvian maize than anything else in our collections. In several peculiar characters they also bear a close resemblance to certain Oriental varieties. These facts reopen the entire problem of pre-Columbian contacts between the New World and the Orient. The actual facts concerning these remarkable plants are summarized below; the questions which they raise are so vast and are in such different fields that even a preliminary discussion of their significance must be a cooperative, long-time program.

Jonathan Sauer has contributed the following note concerning the locality where the ears were collected:

"Chiuchiu is an Indian village on the Rio Loa above Calama. It is an irrigated oasis within the approximately rainless desert, the green valley land surrounded by completely barren plains. The altitude is slightly over 2500 meters, and the latitude 22° South. The site is subject to occasional cold winds blowing across near-by snowy mountains. We saw three kinds of maize at the village, the most largely produced being a yellow flint which is also popped. Flint and pop corns are not clearly differentiated in use, name, or perhaps even as to philogeny. They are commonly lumped by the native name *morocho*. In addition, there was a markedly smaller white *morocho* preferred for popping purposes. This is the sample used by Dr. Anderson in the present study. The third local corn was a white, plump-grained flour corn."

The original collection by Sauer and Sauer consisted of two ears which were essentially similar. One of them is illustrated, approximately natural size, in pl. 18. Measurements on the ear and on the plants grown from the seed are presented in table 1. Diagrams of internode patterns are shown in fig. 1. The ears were small,

TABLE I

MEASUREMENTS OF MAIZE FROM THE RIO LOA

Ear No.	Midcob width	Midear width	Row No.	Shank diam.	Cob color	Leaf width	Leaf length	Plant height	Kernel width
1	1.5 cm.	2.8 cm.	20	6 mm.	red	10 cm.	60 cm.	11 dm.	4 mm.
2	1.1 cm.	2.6 cm.	16	5 mm.	white	8 cm.	60 cm.	9 dm.	4 mm.

with slender cobs, the latter being less indurated than is common in modern maize. They were rounded and tapered toward both ends. The small kernels were so irregularly set that the rows (which are apparently arranged spirally) were difficult to count. As in many South American varieties, the kernels were so lightly attached to the cob that they fell off when the cob was handled. Each of the ears was segregating for endosperm color and showed some white and some light yellow grains. Ear No. 1 had a red cob and No. 2 a white one. Cross-pollinations with tester stocks supplied by E. G. Anderson indicated that they were of the genetic

composition *rrccPrPr*. The kernels were flinty and were rounded at the apex.

Seed from cob No. 1 was planted in early May and matured its tassels in 2½ months. Seed from cob No. 2 was planted in late July, and the plants shed their first pollen in exactly 60 days. This was a much shorter season than any of our other collections from South America. Internode diagrams of five plants are presented in fig. 1. As compared with our other collections, the plants from the Rio Loa are outstanding by the constancy of their internode length and the shortness of the internode below the tassel. On the one hand, they did not have the series of gradually increasing short internodes at the base of the plant; on the other, the central internodes were shorter and less variable.

The leaves were short, wide, and pointed, and were unusual in color and texture. They were very dark green and seemed thicker, smoother, and more flexible to the touch than do ordinary maize leaves. There was no pronounced channel in the middle of the leaves as in North American maize, and the mid-rib scarcely protruded from the under surface of the leaf.

The anthocyanin coloration of the sheath was similar to that of our high-altitude collections from Peru and Ecuador but was more extreme. It was not noticeable in young plants but developed rapidly just before the tassels appeared, starting on the back of each sheath and spreading out from this center. It was a dark brownish red and was deposited between the veins of the sheath. When fully developed it gave the appearance of dark green veins running across a purple-brown background. The color was highly and evenly developed on the back of the sheath and faded out towards the margin so that there was almost no color in the marginal centimeter. Dr. L. J. Stadler informs me that both of these features (avoidance of the margin and interveinal color deposition) are usually indicative of a "strong" allele of *B* and a weak allele of *R*.

In our cultures the plants bore from two to four ears with long narrow blade-like appendages on the outer husks. The development of color in the husks was similar to that in the leaves.

As the plants began to tassel one of their most striking features was the one-sided arrangement of about half of them. On these plants the blades of the upper two or three leaves were displaced so that they were immediately above one another and formed a sort of spathe for the tassel (the male inflorescence) when it first appeared. This peculiar arrangement was first described by Collins ('09) as occurring in some of the Waxy maize from China and Burma and has been supposed to be unique in these Oriental varieties. It is well illustrated in Collins' plate in which the plants look very much like some of ours except that ours have broader leaves. As the plants developed they gradually grew out of this peculiar position, and at maturity almost no indication of the one-sided arrangement was left. So far as we know it has not previously been reported for any New World varieties of maize. However, in our own cultures an approach to this condition is sometimes seen in the peculiar high-altitude varieties from Peru and Ecuador.

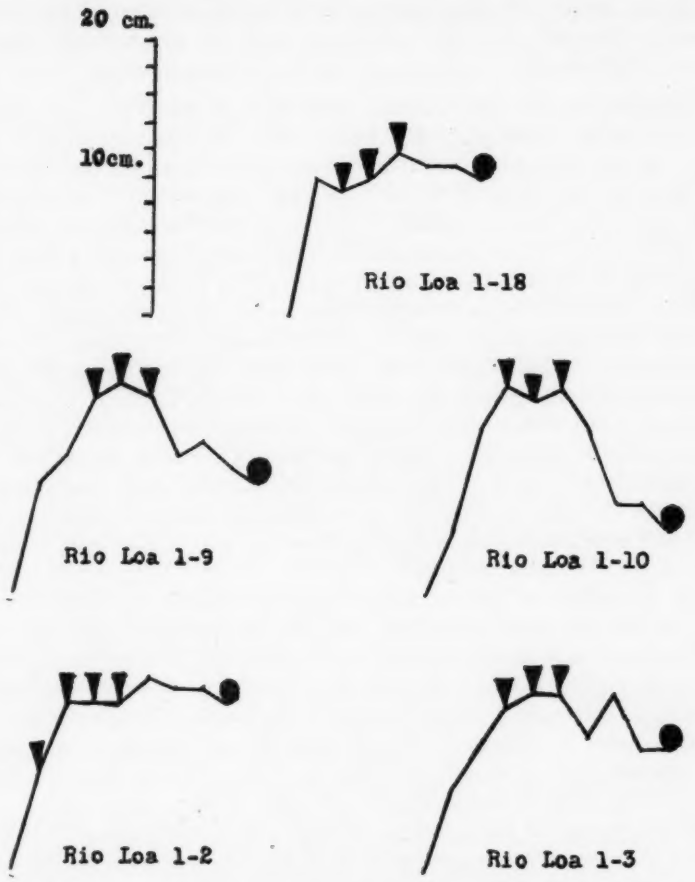

Fig. 1. Internode diagrams of five plants of Rio Loa–1 grown in the experimental fields of the California Institute of Technology at Arcadia, Calif. In each figure the vertical scale represents height in centimeters; the horizontal scale, successive internodes; triangles, ears; and circles, tassels.

The tassels were a dark green throughout, varying from plant to plant in the extent to which a dull dark red was deposited on the glumes, all of which had a bar of dark red at the base. The glumes were small, the upper spikelet was pedicelled, though the length of the pedicel was not as long as in many South American varieties. Several of the plants were sterile, and whether this was due to the change in environment or a segregating gene we have as yet no means of knowing. The plants were segregating for anther and silk color. In some both silk and anthers were pure green; in the remainder they were dilute sun-red.

Pollen mother cells were examined cytologically by means of aceto-carmine smears. They were knobless at pachytene with the exception of chromosome No. 6, which showed a small knob adjacent to the organizing body.

Comparisons with Other Varieties.—The Rio Loa maize as described above was more or less like much of the high-altitude maize of South America in its broad leaves, its low knob number, its tassel characters, and its rounded ears with irregular rows and easily detached kernels. For comparison we had living plants from Peru and Ecuador and an unpublished summary of Bolivian maize prepared by Dr. Hugh C. Cutler. In other characters it is more unique and bears a close resemblance only to certain Oriental varieties and to early prehistoric ears from South America. Contrary to general belief, maize is very extensively grown in certain parts of the Oriental tropics (Heyne, '27; Van Gorkom, '13; Collins, '09) as, for instance, Java, Madura, Burma, and South China. For exact comparisons there are available only the general statements in the literature, Collins' excellent detailed report on a more or less mixed collection from China, and the inbred descendants of this original importation. Seeds of the latter were kindly supplied by J. H. Kempton, then of the U. S. Department of Agriculture. From this material we know that the maize from the Rio Loa resembles the Oriental varieties in its small cob, small seeds, early season, dark green leaves, and in its peculiar habit of forming a spathe over the developing tassel.

Of the prehistoric material, only the ears are available for comparison since they are hundreds if not thousands of years old, and since maize seeds never retain their viability more than a decade or two at the most. The prehistoric material was made available through the courtesy of Professor Alfred Kroeber and the Museum of Anthropology of the University of California. There was also a single collection made by Professor Carl Sauer which was of particular interest since it was obtained from an ancient graveyard only a short distance from the modern maize field in which he found the maize described above.

Distinctive ears of the prehistoric collections are illustrated in pl. 18. It will be seen that the early Nazca material agrees with the ears from the Rio Loa in being small-grained, small-cobbed, irregular-rowed and appressed. All of these ears are associated with the culture designated by archaeologists as "early Nazca." Not until later cultures did larger grains and straighter rows make their appearance (pl. 18, fig. 5). While the ears from the Rio Loa are not identical with the prehistoric collections, they resemble them much more closely than do any of the other ears in our collection, or any that we have seen.

Discussion.—While it has long been known in the Occident that maize was of considerable antiquity in the Orient (see Laufer for a complete discussion) the published evidence could lead only to the conclusion that *Zea Mays* originated in the New World and that it was post-Columbian in the Orient (Mangelsdorf and Reeves, '39). When, however, we no longer content ourselves with cataloguing any kind of maize merely as *Zea Mays* (Anderson and Cutler, '42), it becomes

necessary to re-examine this evidence more precisely. The facts reported above demonstrate that a peculiar strain of maize from a remote and isolated Chilean oasis is, on the one hand, very similar to early prehistoric maize of that same region and, on the other, to certain Oriental varieties. This suggests very strongly a pre-Columbian transfer of maize between the Orient and western South America. From the evidence at present available we have no means of knowing whether it might have originated in the Orient and then spread to South America, there to continue its development as outlined by Mangelsdorf and Reeves ('39) or whether it may have originated in South America and spread in the other direction. All that we know for certain is that a primitive type of maize from western South America is more like Oriental maize in several of its distinctive characteristics than are any of the more commonly cultivated races of that polymorphic species.

It is imperative therefore that the entire problem be re-examined in the light of this evidence and that in particular the small-grained, small-cobbed "pearl Maize" of the Orient be exhaustively compared with living and prehistoric American varieties. Not until extensive collections have been made in Upper India, Burma, and the Dutch East Indies will we be in a position to discuss the question intelligently. It may be pointed out in passing that this region is one of the chief centers of diversity of the Maydeae (Henrard, '31), the group of grasses to which *Zea* belongs. Furthermore, if we follow Mangelsdorf and Reeves ('39) in excepting the genus *Euchlaena* as a comparatively recent artifact, all the Oriental Maydeae agree with *Zea* in having chromosome numbers based on 5 or 10 while the New World Maydeae have a base number of 18.

Summary.—A variety of maize collected from a remote and isolated agricultural community in northern Chile is very similar to the maize of the prehistoric Nazca culture of that same area and adjacent Peru. If not identical with Nazca maize it resembles it more closely than do other varieties in our collections of North and South American maize. In a number of distinctive and peculiar characters it is also more like certain Oriental varieties than anything else in our collections. These facts reopen the entire question of Oriental vs. Occidental origins of *Zea Mays*. Before the problem can be intelligently discussed, definitive collections of maize must be assembled from southern China, Burma, northern India, and the Dutch East Indies.

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EXPLANATION OF PLATE

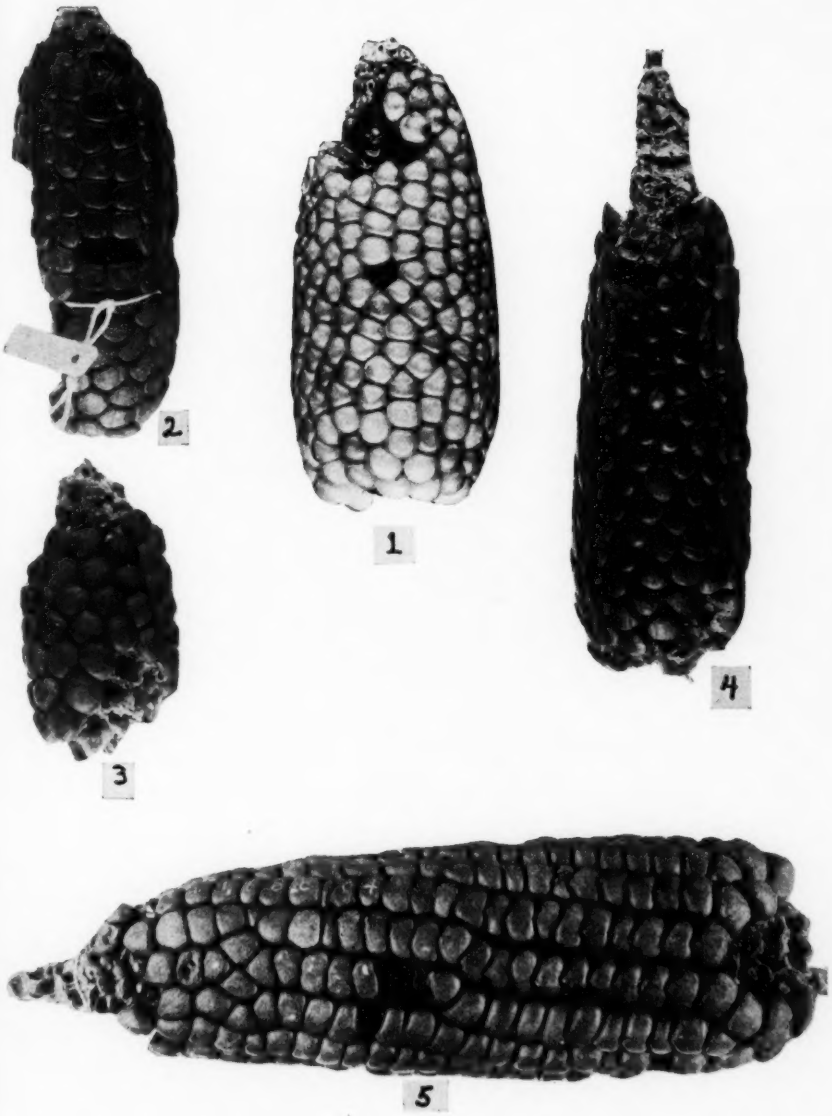
PLATE 18

Figs. 1–5. Rio Loa maize compared with prehistoric South American ears. All approximately natural size. Photographs courtesy of the Museum of Anthropology of the University of California.

Fig. 1. Original ear (No. 1) collected by Sauer and Sauer.

Figs. 2–4. Three ears (No. 171037) collected at Nazca, Peru, by Professor A. L. Kroeber.

Fig. 5. Prehistoric ear from a later period (Late Inca) to show differences. No. 168804 (courtesy of the Field Museum) collected at Lima Valley (Armatambo), Peru, by Professor A. L. Kroeber. Note the larger cob, larger kernels, and straighter rows.



ANDERSON—A MAIZE VARIETY FROM RIO LOA

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